The distribution of Longidoroidea (nematoda) in Europe and variation in the morphology, biology and virus transmission of Xiphinema diversicaudatum (Micoletzky, 1927) Thorne, 1939

Thesis

THE DISTRIBUTION OF LONGIDOROIDEA (NEMATODA) IN EUROPE AND VARIATION IN THE MORPHOLOGY, BIOLOGY AND VIRUS TRANSMISSION OF Xiphinema diversicaudatum (MICOLETZKY, 1927) THORNE, 1939.

BY

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Bachelor of Arts (Open University)

A thesis submitted for the degree of Doctor of Philosophy in the Science Faculty (Biology) of the Open University. The work was done at the Scottish Crop Research Institute, Invergowrie, Dundee under the supervision of Professor C.E. Taylor and with the supervision of Dr. P. R. Thomas of the Open University.

DECLARATION

I hereby declare that the thesis which follows is my own composition, that it is a record of work done by myself and that it has not been presented in any previous application for a Higher Degree. The work was done at the Scottish Crop Research Institute, Invergowrie, Dundee under the supervision of Professor C. E. Taylor and with the supervision of Dr. P. R. Thomas of the Open University.

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CERTIFICATE

We certify that DEREK JOHN FINLAY BROWN, a candidate for the Degree of Doctor of Philosophy in the Open University, has fulfilled the Regulations of the Open University for the Degree of Doctor of Philosophy by Thesis so that he is qualified to submit this thesis.

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ACKNOWLEDGEMENTS

I am most grateful to my supervisors, Professor C. E. Taylor and Dr. P. R. Thomas for all the advice and guidance they have given throughout this study.

I would like to thank Dr. M. Luc and Mr. D. J. Hooper for their advice and helpful comments on taxonomy and Dr. Pauline. B. Topham for advice on statistics. Dr. A. F. Murant is thanked for helpful discussion and for virus serology.

Thanks are also due to Mr. I. M. Roberts for introducing me to immunosorbent electron microscopy; Mr. W. M. Robertson for electron microscopy and Mr. T. G. Geoghegan for photography.

I am indebted to the many individuals who supplied mounted specimens, cultures of nematodes and information relating to this study. Also I thank the Crowther Fund of the Open University for their financial assistance.

The help of Mrs. Jean Findlay with typing and Mr. R. J. Clark with computer type-setting is gratefully acknowledged.

Finally I wish to thank Professor C. E. Taylor, Director, Scottish Crop Research Institute for allowing me to use the facilities of the Institute.

Non-indigenous viruses and nematode populations were held at the SCRI by courtesy of a Department of Agriculture and Fisheries for Scotland licence.

To

June, Derek and Richard.

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Abstract

The geographical distributions in European and Mediterranean countries of 58 species in the Longidoroidea are shown on standardised format maps. This information and interspecific variability in the Longidoroidea is used to form groups of nematodes each group generally consisting of an amphimictic species and several thelytokous species. The possibility is discussed that within each group the thelytokous species may have evolved from the ancestral amphimictic species.

An examination of intraspecific variability between populations of Xiphinema diversicaudatum from Europe, USA and New Zealand revealed much significant variation in their morphometrics and populations could be grouped according to their morphological similarity. Methods of killing, fixing and processing specimens to glycerol, the microscope-measuring system, operator recording measurements and changes in biotope altered significantly the morphometrics of X. diversicaudatum. Differences occurred in the proportions of males and females in populations of the species and, using a standard test system, populations were found to have different reproductive capacities. However, females from the populations successfully crossbred with males from a Scottish population and produced viable F1 and F2 hybrids which confirmed the populations belonged to the same species.

Strains of arabis mosaic and strawberry latent ringspot (SLRV) viruses were transmitted, each with a different degree of efficiency, by populations of X. diversicaudatum and specificity of transmission existed between each virus strain and each nematode population. Different virus source and bait- plants affected the efficiency with which viruses were transmitted and a strain of SLRV from Italy was transmitted consistently only by a population from Italy. Infrequent or non-transmission of viruses by nematodes resulted from an inability

of the nematodes to adsorb and retain virus particles at specific sites. A study using parental and F1 and F2 hybrid X. diversicaudatum revealed that the nematodes ability to adsorb and retain virus particles was hereditary and that different maternal and paternal parents could affect the potency of the hybrids as virus vectors.

Results from this research programme form a basis with which to compare interspecific variability in the Longidoroidea.

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I hereby declare that the text, tables, figures and bibliography which comprise my thesis entitled "The Distribution of Longidoroidea (Nematoda) in Europe and Variation in the Morphology, Biology and Virus Transmission of Xiphinema diversicaudatum (Micoletzky, 1927) Thorne, 1939." may be used, lent or photocopied by the Open University exclusively at their discretion. No part of the thesis referred to above may be published or used in any publication without prior permission being granted in writing by the author.

Yours sincerely,

Derek J.F. Brown

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CHAPTER I

PREFACE

Interest in members of the superfamily Longidoroidea increased after Hewitt et al. (1958) reported Xiphinema index to be a vector of grapevine fanleaf virus. Several further discoveries of other Xiphinema and Longidorus species able to transmit a range of plant viruses followed this initial record of a soil-borne plant virus having a plant parasitic nematode as a vector. As a result of this new interest in the Longidoroidea much information has been reported about the presence and absence of longidoroid nematodes in many parts of the world, particularly European and Mediterranean countries.

More than 90% of the species in the Longidoroidea have been described since 1958 and it may be anticipated that many further species have yet to be identified. Most species appear to be thelytokous (=constant parthenogenesis; parthenogenesis = asexual reproduction) but a few are considered amphimictic (= sexual reproduction). The morphological species concept, by general agreement, is used by taxonomists to ascribe populations of longidoroid nematodes to specific rank (Stone, Platt and Khalil, 1983). This reliance on morphological and morphometric differences to determine specific rank has caused doubts about the systematics of some members of the Longidoroidea. At a NATO Advanced Study Institute on "Nematode Vectors of Plant Viruses" held at Riva dei Tessali, Italy, during May, 1974, it was suggested that a study be undertaken to examine intraspecific variation present in an amphimictic species in the Longidoroidea. It was hoped that the results of such a study could be used as the basis for comparing interspecific variation in the Longidoroidea, especially between thelytokous species.

The following research programme was undertaken in response to the suggestion made at Riva dei Tessali. The research programme is

divided into five inter-relating Parts, the first (Chaps. II, III and IV) being a review of selected references recording the geographical distribution of members of the Longidoroidea. This part also includes a discussion as to how these data combined with morphological data may be used to form groups of species in the Longidoroidea present in European and Mediterranean countries. Part II (Chaps. V, VI, VII and VIII) deals with intraspecific morphometric variation in X. diversicaudatum and includes details of the effects on morphometrics of:- methods used to prepare specimens for examination by optical microscopy; geographical distribution and changes in biotope. Part III (Chap. IX) deals with variation between populations of X. diversicaudatum in their sex ratios and in their abilities to breed and crossbreed under standard conditions. Part four (Chap. X) deals with variation in the abilities with which different populations of X. diversicaudatum are able to transmit strains of arabis mosaic and strawbery latent ringspot viruses. Also examined are some factors affecting the transmission of these viruses and the possibility that the nematode's ability to transmit virus may be inherited. Part five (Chap. XI), is an Apercu in which the results from the study are reviewed and the present difficulties of speciation in the Longidoroidea are discussed; it is suggested that two separate concepts of speciation may be applied to the Longidoroidea - one for the thelytokous species, and another for the amphimitic species.

It is hoped that this research programme fulfills the suggestion made at Riva di Tessali and that the information presented can be used as a basis for further study comparing interspecific variability in the Longidoroidea.

PART ONE

"DISTRIBUTION"

CHAPTER II

THE LONGIDOROIDEA OF EUROPE

II 1. INTRODUCTION

The order Dorylaimida Pearse, 1942 comprises two suborders which contain all of the currently known virus vector species. The suborder Diphtherophorina, which contains the trichodorid virus vector nematode species, is not discussed in this study.

The suborder Dorylaimina has, at present, one superfamily, three families, three sub-families, eight genera, 205 species and several other species inquirendae or species incertae sedis.

Recently Khan et al (1978) gave a classification of nematodes in the former "Longidorus - Paralongidorus - Xiphinema" complex. Their classification (Fig. 1), amended by the inclusion of an unnamed genus proposed by Khan (1978), is used in this present study.

Although several reports existed of longidoroid (= species in the superfamily Longidoroidea) nematodes associated with poorly growing plants, the first record of direct damage to a plant root caused by one of these nematode species was not published until 1954. Horner and Jensen (1954) reported finding a Longidorus sp. associated with extensive stunting and death of peppermint (Mentha piperita) throughout many of the older mint growing areas of western Oregon, USA. They also reported experiments in which the Longidorus sp. was shown to cause stunting and a root die-back condition of peppermint. Schindler (1957) gave a detailed account of the pathogenicity of Xiphinema diversicaudatum on strawberry (Fragaria sp.) and the following year Hewitt et al. (1958) reported the first evidence of the plant parasitic nematode - X. index - transmitting a plant virus - grapevine fanleaf virus. In Europe, Jha and Posnette (1959) and Harrison and Cadman (1959) reported that arabis mosaic virus , which was causing a disease in strawberries in southeastern England , was

transmitted by X. diversicaudatum. These and other reports of plant parasitic nematode species transmitting plant viruses (Taylor and Brown, 1981) stimulated renewed interest in the taxonomy, morphology and biology of the Longidoroidea. This has resulted in almost 90% of the presently known longidoroid species having been identified and described since 1958 (Fig. 2).

At present 22 longidoroid species have been implicated as vectors of 19 viruses and several serologically distinct strains of some of these viruses (Fig. 3: Taylor and Brown, 1981; Forer and Stouffer, 1981; Roca and Lamberti, 1981; Eveleigh and Allen, 1982). Trudgill, Brown and McNamara (1983) re-examined the evidence contained in all of the published reports describing longidoroid nematodes transmitting plant viruses and virus strains. They concluded that adequate published evidence was available to suggest that only 12 viruses and virus strains were transmitted by 9 longidoroid species. However, several viruses, similar to existing nematode transmitted viruses, have as yet no known vector and few of the 205 species in the longidoroidea have been studied in any detail. Therefore, it is likely that some of these species or species not yet identified may be implicated as vectors of known or as yet unidentified viruses or virus strains.

The earliest records of longidoroids are Dorylaimus maximus (Butschli, 1874) and D. elongatus (de Man, 1876) now referred to Siddiqia maximus and Longidorus elongatus respectively. In 1922 Micoletzky included these two species in the subgenus Dorylaimus (Longidorus) but Filipjev (1934) subsequently raised Longidorus to generic rank in the family Dorylaimidae de Man, 1876. The first list of species in the genus Longidorus was given by Thorne and Swanger (1936).

Longidorus diversicaudatum was first described by Micoletzky (1927) and subsequently was transferred to the genus Xiphinema by Thorne (1939). However, Cobb (1913) first erected the genus Xiphinema with the type species X. americanum.

These and other reports of longidoroids prior to 1958 were mainly the result of random explorations or faunistic studies made for zoological purposes. However, after 1958 many of the new records of longidoroids were a result of field, faunistic, taxonomic and biology studies closely connected with agriculture or horticulture. The results from surveys, specifically designed to identify the occurrence and abundance of longidoroids present in a particular crop, area or country steadily increased in number from the mid 1960's (Cohn, 1969; D'Herde and van den Brande, 1964; Weischer, 1966; Wyss, 1969 a and b). More recently considerable interest has been shown in the geographical distribution of longidoroids, particularly in Europe, North America and India (Anon, 1978; Brown et al., 1978; Bajaj and Jairajpuri, 1979). In Europe surveys have been carried out in several countries and the results from some of these surveys have been discussed in a European context (Dalmasso, 1970; Taylor and Brown, 1976). Also, atlases of the distribution of longidoroids have been published for Britain (Brown and Taylor, 1977), Spain (Arias, 1979), The Netherlands (Seinhorst and van Hoof, 1982) and, with a few longidoroids, for Europe (Brown, Boag and Taylor, 1981).

Increasing interest in Europe during the 1970's of longidoroid nematodes and the biogeography of nematodes resulted in the formation of a small group of interested nematologists to examine the possibility of a European nematode survey. The European Plant Parasitic Nematode Survey scheme formally began in 1978 with the publication of a guide for contributors to the scheme (Brown et al.,

1978). In the following year the European Science Foundation agreed to financially support a modified scheme restricted mainly to member countries of the Foundation.

This present study primarily uses existing, selected, published, records of the occurrence of longidoroid nematodes in all European and Mediterranean countries, excluding the Union of Soviet Socialist Republics (USSR). By collating and mapping the data contained in such reports the European distribution of longidoroid nematodes can broadly be defined and is presented here.

II : 2 MATERIALS AND METHODS

II : 2 : 1 European countries

For the purposes of the present study Europe is broadly defined to include all European countries, Mediterranean islands and North African countries abutting the Mediterranean sea. Jordan is also included due to its relatively close proximity to the Mediterranean sea but the USSR, with its component states e.g. Moldavia, Ukraine, Uzbekskaya, etc., is not included.

Mediterranean islands such as Sardinia, Corsica and Sicily which come under the jurisdiction of a country abutting the Mediterranean sea are included with the appropriate country e.g. Rhodes with Greece, Corsica with France, etc. The island of Cyprus is treated as one complete entity and the countries comprising Britain, although centrally governed, are each treated as equivalent to other autonomous European countries.

II : 2 : 2 Data sources

Many nematologists throughout Europe have much unpublished data concerning the occurrence and distribution of Longidoroidea in their

own and often other European countries. However, to avoid any accusation of plagiarism the present study refers, with few exceptions, only to published data which are appropriately acknowledged, usually in the Figure legends. Therefore, much information is necessarily excluded from the study. In a few instances, where a species of particular interest has been recorded but the discovery has not been published, the source of information is quoted.

Data relating to the distribution of Longidoroidea in Europe are contained in several hundreds of publications which appear in many different scientific journals. The quality of the data contained in these research papers varies from simple presence or absence information of a particular species from a generalised area to very precise details of the exact location, population size, host crop and virus association , if any, for the species. Some maps, also have been published showing the distribution of selected nematode species within a country or area, but generally the maps are inaccurately drawn and give imprecise information of the distribution of the nematode species presented.

In several countries the results of surveys and literature reviews are published as atlases containing standardized maps showing the distributions of Longidoroidea (Arias, 1979; Brown and Taylor, 1977; Dalmasso, 1970; Seinhorst and van Hoof, 1981). For these countries the atlases are used as the primary source of data for the study and other publications from these countries are only used if they contain additional information.

Although information is available concerning the Longidoroidea in the USSR much of it relates only to a few scattered areas of the country i.e. information is available for Moldavia (Koev et al., 1971) Moscow area (Romanenko, 1971) Tadzhikistan (Ivanova, 1972) and Ukraine

(Milkus et al., 1974, 1975). Little or no information is available for many areas e.g. Lithuania, White Russia, etc. Kiryanova and Krall (1969) cite 2877 titles of nematological papers published in the USSR up to 1966. Several of the papers cited contain information about Longidoroidea in the USSR but many of these papers are unobtainable. Because of the lack of availability of relevant research papers the USSR is not included in the study. However, the occurrence of Longidoroidea in the USSR, recorded in over 50 selected research publications, is reported in a subsequent chapter (see Chapter III).

The Helminthological Abstracts, 1931 to mid-1982 have been scanned for references to Longidoroidea in Europe and these were then checked in the original publications. Data were also obtained from other publications not included in Helminthological Abstracts and from publications kindly supplied by nematologists in Europe.

The study does not purport to include all published data pertaining to Longidoroidea in Europe. Because of the diversity of European journals containing nematological data; the many different European and Mediterranean languages; the absence of sufficient data in many publications and the repetition of data in several publications, only about 150 selected papers were used in the study. However, the information available from these papers enabled maps to be completed of the distributions of the European Longidoroidea.

II : 2 : 3 Mapping

The distributions of the European Longidoroidea are presented on standardised, pre-printed, base-maps of Europe, as used by the European Invertebrate Survey (Monks Wood Experimental Station, Abbots Ripton, England). Each map consists of the outline of Europe, country borders, major rivers, lines of latitude and longitude and the sea areas, which are stippled. The appropriate section of the Universal

Transverse Mercator map projection system, using map squares representing 50 km squares derived from the conventional map squares representing 10 km squares, is superimposed and printed, in a different colour, on the base-map. Lettraset (London, England) symbols representing the nematode species were added, by hand, to the base-maps in the appropriate central position within a 50 km map square.

When a map was completed the superimposed printed map grid was removed photographically from the final maps. Therefore, the final maps contain only the outline of Europe, country borders, major rivers, lines of latitude and longitude, the stippled sea areas and the symbols representing the species distributions on a 50 km map square basis.

The distributions of longidoroid species in Europe have been plotted as accurately as possible but references used for the study often have insufficient or imprecise details of species locations. Therefore, accurate plotting has not always been possible. However, the area covered in the study, as represented on the distribution maps, is 16,000 sq. km (4,000 sq. km x 4,000sq. km). Therefore, assuming that the distribution point is incorrectly plotted and placed in an adjoining 50 km map sqaure, the resultant error in the area covered in the study is calculated as being 1.25% north or south and 1.25% east or west.

II : 2 : 4 Longidoroidea nomenclature

In the superfamily Longidoroidea Khan et al. (1978) the families, subfamilies and generic names of Khan et al. (1978) are used in this study. Also, the specific names in the Paralongidorus and Siddiqia genera as given by Khan et al. (1978) are used. However, Khan et al. (1978) did not give a list of species in the Xiphinema genus. Further, their list of Longidorus species is incomplete as several

well documented species are omitted without any reasons or explanation given for the authors decision. Therefore, the lists of Longidorus and Xiphinema species given by Hooper and Southey (1978) are used in the study but with the addition of L. cylindricaudatus, L. fasciatus and L. intermedius in the Longidorus species list and X. algeriense, X. dentatum, X. globosum and X. israeliae. X. mediterraneum is a junior synonym of X. pachtaicum (Siddiqi and Lamberti, 1977) therefore the latter specific name is used in this study.

Species synonyms of particular interest to the present study are discussed where appropriate in the results section.

II : 3 RESULTS

II : 3 : 1 Longidorus species present in Europe

As a pre-requisite before starting the present study the assumption had to be made that all identifications of species, reported in the publications used for the study, were correct. It is acknowledged that some misidentifications may be contained in some of the publications, it was not feasible to check these and all records therefore remain as published.

From the total of 29 Longidorus species reported to occur in Europe at least one species is present in 27 of the 36 European countries from which Longidoroidea have been reported (Tab. 1). France and West Germany each have 12 Longidorus species present which is the largest number of Longidorus species reported from any individual country. Eight Longidorus species reported to be virus vectors (Taylor and Brown, 1981) are present in Europe and in 22 countries at least one of these species is reported present.

II : 3 : 2 Paralongidorus species present in Europe

Only one Paralongidorus species is reported from Europe (Tab. 2) namely P. georgiensis from the river Nile delta and near Port Said in Egypt.

II : 3 : 3 Siddiqia species present in Europe

Three Siddiqia species are reported to occur in Europe (Tab. 2). Two species S. epimikis and S. remeyi have been reported only from Algeria and France respectively. However, S. maximus, which has been reported to transmit viruses under laboratory conditions, has been reported present in 11 European countries.

II : 3 : 4 Xiphinema species present in Europe

Of the 116 described species in the genus Xiphinema 24 species are reported present in 36 European countries (Tab. 2). The number of species present in individual European countries ranges from only one species present in nine countries, to a maximum of 13 species in Spain. The mean number of species present in countries abutting the Mediterranean sea is 5.4 and in those countries abutting the North Sea and English Channel is only 3.1.

Eight Xiphinema species reported from European countries have been recorded as virus vectors (Taylor and Brown, 1981) but it is possible that only four of these species may be virus vectors (Trudgill et al., 1983). At least one of the virus vector species is present in 34 of the 36 countries reported to have Xiphinema species present. The mean number of species present in countries abutting the Mediterranean sea is 5.4 and in those countries abutting the North Sea and English Channel is only 3.1.

II : 3 : 5 The European Longidoroidea and the European countries in which they occur

The 28° Longidorus species, three Siddiqia species, one Paralongidorus species and 25 Xiphinema species reported to occur in Europe are given in Tab. 3, each with a list of the European countries from which they have been reported. Longidorus elongatus occurs in most European countries having been reported from 19 countries. Of the Xiphinema species, X. pachtaicum and X. diversicaudatum are most frequently reported with reports from 24 countries and X. index is reported from 19 countries.

II : 3 : 6 The European countries and the Longidoroidea present in them

The 36 European countries from which Longidoroidea have been reported are given in Tab. 4 together with a list of the Longidoroidea which have been reported to occur in each of them. European countries for which there are no reports of the occurrence of Longidoroidea are also given in Tab. 4.

It cannot be surmised whether Longidoroidea exist in any of the other nine countries listed as having no Longidoroidea present (Tab. 4) as little or no information is available.

Two European countries, Malta and Morocco, only have one Longidoroid, X. pachtaicum, reported present but 25 Longidoroidea are reported from France; this being the largest number of Longidoroidea reported from any individual European country.

II : 3 : 7 The European distribution of Longidorus species

Longidorus africanus (Fig. 4):

All populations of L. elongatus reported from North Africa are now referred to L. africanus (Lamberti, 1975). Therefore, L. africanus has been recorded in four Mediterranean countries; Egypt,

where it is present in soils from the Nile delta; Greece from one sample from Preveza county; Israel, in soil samples from the central region and coastal strip and from Jordan from the central valley. An L. africanus intersex female, with well developed male spicules, was identified from the rhizosphere of avocado (Persea gratissima) in Israel (Cohn and Mordechai, 1969).

Longidorus apulus (Fig. 4):

There are several published reports of L. attenuatus occurring in mainland Italy, Sardinia and the Yugoslavian island of Vis (Lamberti et al., 1973; Prota et al., 1971; Rana and Roca, 1973; Roca et al., 1975; Roca et al., 1975; Taylor et al., 1976; Vovlas and Roca, 1975). However L. attenuatus reported from Sardinia is referred to L. protae and the other reports of L. attenuatus are now referred to L. apulus (Lamberti and Bleve-Zacheo, 1977). In the Bari and Brindisi areas L. apulus is common, being reported from 42% and 16% of soil samples respectively. But in the Foggia area L. apulus was found to be present in only 4% of soil samples and is believed to have been introduced to the area in soil adhering to artichoke sprouts (Cynara scolymus) used for propagation (Roca et al., 1975). Also, in southern Italy L. apulus causes much damage, especially to artichoke crops, by transmitting artichoke Italian latent virus and the associated chicory chlorotic-ringspot strain (Vovlas and Roca, 1975; Roca et al., 1975).

Longidorus attenuatus (Fig. 4)

This species has a restricted or localized distribution in the eight European countries from which it has been recorded. In Italy L. attenuatus has been reported to transmit virus to artichoke but these reports are now referred to L. apulus as is a report of L. attenuatus from Yugoslavia. Also a report of L. attenuatus from

Sardinia is now referred to L. protae (see L. apulus).

Thorne (1939) described L. elongatus from soil associated with fig tree roots from Syrna, Turkey and Hooper (1961), when redescribing L. elongatus, stated that Thorne's report was probably correct. According to Sturhan (1963a) the morphometrics and expanded lip region reported by Thorne (1939), might also suggest that the specimens were L. attenuatus. Also, Sturhan (1963a) considered it unlikely that specimens of L. elongatus from the USA, also described by Thorne (1939), were L. elongatus or L. attenuatus. It may be speculated that Thorne's (1939) L. elongatus from the USA were L. breviannulatus (Norton and Hoffmann, 1975) but Thorne's (1939) specimens were males and males of L. breviannulatus were not found in the type population. Lamberti (1975) records that Thorne's (1939) Turkish specimens of L. elongatus were not synonymous with L. attenuatus but no details are given for rejecting the possible synonymy. Thorne (1939) presented a figure of the head region of a Turkish female specimen of L. elongatus which shows the specimen to have an expanded lip region unlike L. elongatus sensu stricto. Also, three of the five morphometrics do not correspond with similar morphometrics of L. elongatus sensu stricto. However, the details given for the Turkish specimens correspond with similar details given for L. apulus Lamberti and Bleve-Zacheo, 1977; also the same morphological details correspond with those of L. attenuatus, L. protae and L. vineacola except for the ratio c measurement. Therefore, Thorne's (1939) L. elongatus reported from Turkey should be considered an identification inquirenda until the specimens can be re-examined and identified.

It seems likely that L. attenuatus may have a limited distribution in Europe, being present only in Belgium, England, West Germany and the Netherlands. Populations of Longidoroidea identified as L. attenuatus in Bulgaria, southern France, Spain and Poland should be

re-examined as they may be species other than L. attenuatus as these populations appear to occur outwith the distribution area of L. attenuatus.

In England L. attenuatus transmits the English strain of tomato blackring virus (TBRV-E; Harrison et al., 1961) and also the lettuce ringspot and celery yellow vein strains of the virus. A virus serologically similar to TBRV-E is transmitted to field pumpkin (Cucurbita pepo; Forgahni et al., 1965) and grapevine (Vitis sp.; Rudel, 1977) by L. attenuatus in West Germany. However, an associated strain of TBRV-E found in Germany, serologically similar to the potato bouquet strain was not transmitted by an English population of L. attenuatus although the population did transmit TBRV-E, lettuce ringspot and celery yellow vein (Trudgill and Brown, unpublished results).

Longidorus caespiticola (Fig. 5):

The distribution of L. caespiticola ranges north to south from southern Scotland to Sardinia and east to west from southern Poland to central Spain. It has most frequently been recorded in soils in England and Wales where it is commonly associated with X. diversicaudatum, and from northern France, The Netherlands, Belgium and southern West Germany. Populations of L. caespiticola from Belgium were reported to have shorter spears and tails and differences in the numbers of body pores and supplements compared with the type population (Aboul- Eid, 1970; Sturhan, 1963a).

Valdez (1972) reported L. caespiticola to be a vector of the English strain of raspberry ringspot virus and the type strain of arabis mosaic virus. Also, Flegg (1969a) reported L. caespiticola as a possible vector of cherry leaf-roll virus but Jones et al., (1981) were unable to transmit the cherry, rhubarb and golden elderberry strains of cherry leafroll virus with L. caespiticola. In limited

experiments L. caespiticola did not transmit the hop strain of arabis mosaic virus and no correlation was observed in the field between L. caespiticola and this virus (Anon, 1969, 1970). McNamara (1978) suggested that the "transmissions" recorded by Valdez (1972) with L. caespiticola might have been due to contamination of the bait plant root systems with virus infected faeces or with nematodes containing ingested virus. Because of the absence of any association of L. caespiticola with virus infections in the field and the possibility that the reported transmissions were caused by contamination it is concluded that L. caespiticola is probably not a virus vector species (Trudgill et al., 1983).

Longidorus closelongatus (Fig. 5)

L. closelongatus was originally described from specimens recovered from soil from virus diseased grapevines in Bulgaria (Stoyanov, 1964). Choleva (1975) reported L. closelongatus in 61% of soil samples from grapevine, damewort (Sambucus ebulus) and nettle (Lamium sp.) in alluvial and forest drift soils in two different regions of Bulgaria. However, in an erratum Choleva (1975) expressed doubt about the identification of the species and that the report should not be regarded as an authentic record of L. closelongatus in Bulgaria. It is relatively common in southern France where it replaces L. elongatus but Dalmasso (1970) included L. closelongatus in the L. elongatus species complex when presenting the results of his survey of the Longidoroidea present in France. However, the distribution of L. closelongatus in France is given in Fig. 5 from data supplied by A. Dalmasso (pers. comm.).

Longidorus cohni (Fig. 4):

L. cohni has only been reported from the Sharon region of central Israel where, due to damage caused by its direct feeding, it was

recognised as a distinct limiting factor of oat (Avena sativa) production (Cohn and Ausher, 1973).

Longidorus congoensis (Fig. 6):

In Europe L. congoensis is recorded only in Algeria and only in soils associated with date palm (Phoenix dactylifera) at four oases, although soil samples from many crop and fodder plants were examined (Lamberti et al., 1975).

Longidorus cylindricaudatus (Fig. 5):

This species has been recorded from four European sites, near Wolfhezen and at Vortum in The Netherlands, Lower Saxony, West Germnay and several sites in Belgium (De Waele, pers. comm.; Kozlowska and Seinhorst, 1979; Rau, 1975). L. cylindricaudatus is similar to L. elongatus but can be differentiated from the latter by its longer odontostyle, shape of lip region and shape of tail.

Longidorus elongatus (Fig. 7):

Many early European records of L. elongatus are now referred to other species e.g. L. elongatus (Oteifa and Tarjan, 1965; Tarjan, 1964a) = L. africanus (Lamberti, 1975); L. elongatus (Thorne, 1939) = species inquirendae (see L. attenuatus); L. elongatus (Goodey, 1951) = L. goodeyi (Hooper, 1961); conversely records of other nematodes are now referred to L. elongatus e.g. Dorylaimus tenuis (Linstow, 1879) = L. elongatus (de Man, 1884); L. monohystera (Altherr, 1953) = L. elongatus (Sturhan, 1963a). This species is commonly regarded by taxonomists as a species complex. Males are rare, therefore reproduction in the majority of L. elongatus populations is probably by mitotic parthenogenisis but bisexual populations have been recorded in France, The Netherlands and West Germany. Morphometric variability occurs between populations of L. elongatus. Sturhan (1963a) reported that some West German populations of L. elongatus had shorter bodies

and odontostyles than the type British population and Dalmasso (1970) reported variation between French populations in the body size and the form of the labial contour. Because of the variation in these French populations of L. elongatus the northern French populations can be grouped with populations from Britain and The Netherlands whereas southern French populations form an easily recognisable separate grouping. Dalmasso (1970) recognised L. elongatus as a species complex and therefore presented the French distribution of the species by referring to it as L. elongatus sensu lato, which also included L. closelongatus. In Scotland a population of L. elongatus was found to contain some intersex females with poor to well developed spicules and the ratio of females to males was 1 to 0.014 and the ratio of females to intersexes was 1 to 0.00015 (Raschke and Boag, 1981).

In Britain the earliest records of L. elongatus are from north east Scotland where it was found in soil samples from pastureland (Robertson, 1928, 1929). A recent survey has shown that the species is widespread and common in eastern Scotland (Taylor and Brown, 1976). L. elongatus has frequently been identified from northern European countries but it has not been reported from central Europe or the Mediterranean coastal areas except for isolated population outliers in Italy and Greece. The populations from Italy and Greece probably refer to another species, as also do populations of L. elongatus from Bulgaria which may have been mis-identified. Similarly records of L. elongatus from Spain and Poland are also of doubtful validity and specimens should be re-identified. At present the European distribution of L. elongatus probably includes the British Isles, Scandinavian countries, East and West Germany, The Netherlands, Belgium and northern France. It is probable that as the L. elongatus species complex is identified into its component parts several new species may be named which in turn may reduce the existing European

distribution pattern for L. elongatus.

L. elongatus causes damage to a wide range of crops by its direct feeding but is more important economically because of the viruses which it can transmit, namely, the English and Scottish strains of raspberry ringspot and the Scottish strain of tomato blackring viruses (Taylor and Brown, 1981). Carnation ringspot virus, a member of the tombuvirus group (Harrison et al., 1971), has been reported to be transmitted by L. elongatus (Fritzsche et al., 1979) but Trudgill et al., (1983) question this.

Longidorus euonymus (Fig. 5) :

Mali and Hooper (1974) first described L. euonymus from several locations in eastern Czechoslovakia and the nematode was reported to be a vector of euonymus mosaic virus which was causing damage to spindle trees (Euonymus europeaus). However, this virus, which is serologically related to tobacco necrosis virus, is known to be transmitted by the fungus Olpidium brassicae which is also associated with the virus in Czechoslovakia. Therefore, it is concluded that L. euonymus is unlikely to be a virus vector species. Szczygiel (in litt.) has found L. euonymus in soil samples from southern Poland and it may be that L. euonymus has a small discrete distribution encompassing southern Poland and Czechoslovakia. However L. euonymus has also been recorded from several locations throughout Bulgaria. If this species identification is confirmed the distribution area of L. euonymus should perhaps be extended to include several eastern European countries.

Longidorus fasciatus (Fig. 5)

Roca and Lamberti (1981) described L. fasciatus from specimens collected from artichoke fields (Cynara scolymus) in Greece and Sicily. The nematode was associated with outbreaks of artichoke Italian latent virus in the field crops and laboratory tests confirmed

that L. fasciatus was a vector.

Longidorus globulicauda (Fig. 8)

Dalmasso (1970) reports this species is established at several localities in Brittany, France which constitute the only records of its occurrence.

Longidorus goodeyi (Fig. 6):

The European distribution of L. goodeyi appears to be restricted mainly to the British Isles, The Netherlands, northeastern France and sporadically in West Germany. It has also been reported from Spain and Bulgaria but these identifications appear to refer to discrete population outliers from the distribution area of the species. Therefore, specimens used for identification from these sites should be re-examined to confirm the original identification. Some populations of L. goodeyi in The Netherlands differed from the type description in the shapes of their amphidial pouches and vagina; the positions of their lateral pores and oesophageal dorsal gland nuclei; and in their vaginal musculature (J.W. Seinhorst, in litt.; Senihorst and van Hoof, 1982). Also, L. goodeyi populations in France differed from the type specimens by having smaller body lengths, less rounded tails and a narrower cephalic profile (Dalmasso, 1970).

Longidorus intermedius (Fig. 6):

L. intermedius resemble L. elongatus but differ from the latter species in having a longer odontostyle, a rounded lip region, more anterior lateral, dorsal and ventral pores relative to the spear guiding ring, the amphids often being slightly bilobed and the absence of thickening of the body in the anal region (Kozlowska and Seinhorst, 1979). The species has only been recorded from several biotopes in The Netherlands, in the Ems valley and Lower Saxony in West Germany and from several sites in Belgium.

Longidorus juvenilis (Fig. 6):

This species has a limited distribution in south eastern France and northwest Italy where it is associated with grapevine, citrus and Pinus strobus.

Longidorus laevicapitatus (Fig. 6):

L. laevicapitatus is relatively host specific, most frequently reported in association with sugarcane (Saccharum officinarum) in tropical and sub-tropical countries (Lamberti, 1975). In Europe this species is reported from four Mediterranean countries and has been found associated with citrus in Egypt and Israel (Oteifa and Tarjan, 1965; Cohn, 1969). Dalmasso (1970) speculates that the species may have been introduced to southern France during an abortive attempt to establish a sugarcane industry there in the 16th century.

Longidorus leptocephalus (Fig. 9):

The type specimens of L. leptocephalus refer to a small form of the species. A large form was recognised by Flegg (1967) and described by Hooper (1973). Hooper et al., (1973) were unable to differentiate the large and small forms using electrophoretic techniques. It is now recognised that the small form is relatively rare and that the large form is most often identified from soils. However, populations intermediate between these two forms also exist and it is not always possible to assign individual specimens to a particular form. In the Scandinavian countries only the large form has been identified.

L. leptocephalus has a very restricted distribution including the Scandinavian countries, northern West Germany, Belgium, The Netherlands and the British Isles. In Britain L. leptocephalus is

frequently found associated with L. elongatus and L. goodeyi but has not been recorded north of the Caledonian Canal in Scotland and shows a preference for soils in the drier, eastern side of Scotland and England (Taylor and Brown, 1976). L. leptocephalus has been recorded from southern Poland and southern West Germany but these populations appear to lie outwith the restricted distribution of the species and therefore perhaps should be re-identified.

Valdez (1972) reported L. leptocephalus to be a vector of the English strain of raspberry ringspot virus and Flegg (1969) recorded L. leptocephalus in association with cherry trees infected with cherry leaf roll virus. Trudgill et al., (1983) suggest that the "transmissions" reported by Valdez (1972) were probably due to contamination of the bait plant root systems and thus L. leptocephalus is not considered to be a virus vector species.

Longidorus macrosoma (Fig. 8):

L. macrosoma is reported from 12 European countries and is relatively common in five of them namely England, France, Belgium, The Netherlands and West Germany. It has only infrequently been identified from soils in Czechoslovakia, East Germany, Eire, Italy, Spain and Yugoslavia. In France L. macrosoma is present in the warmer lower lying areas and is mainly absent from the cooler higher altitudes where L. caespiticola and L. profundorum replace it (Dalmasso, 1970). A population of L. macrosoma from southern England has been successfully maintained for several years in its natural soil, with raspberry as the plant host, in an out of doors microplot at the SCRI, Dundee.

Rau (1975) recorded L. macrosoma and X. diversicaudatum from shallow soil covering the slopes and top of a carboniferous limestone

ridge on which natural vegetation, beech and grasses, were growing in lower Saxony, West Germany. Taylor et al. (1978) reported that in southern England L. macrosoma possibly was associated with the distribution of calcareous soils and underlying rocks of the Jurassic and Cretaceous periods and also with the southern limit of the last glaciation. However, Taylor and Brown (1976) suggested, that in Britain, the distribution of L. macrosoma was associated with the distribution of ancient deciduous woodlands. McNamara and Flegg (1981) subsequently supported this suggestion and associated the British distribution of L. macrosoma with prehistoric-British oak (Quercus robur) and beech (Fagus sylvatica) forests.

A female intersex with rudimentary male characteristics but with spermatozoa in the uterus and spermatheca, suggesting that copulation had occurred, has been recorded from a Belgian population of L. macrosoma (Aboul-Eid and Coomans, 1966).

Five viruses have been reported to be transmitted by L. macrosoma (Taylor and Brown, 1981) but Trudgill et al. (1983) suggest that published evidence is valid only for the transmission of the English strain of raspberry ringspot virus. L. macrosoma has been shown by electron microscope studies, to retain virus particles of both the English and the Scottish strains of raspberry ringspot virus (Taylor and Robertson, 1973). The nematode only rarely transmits the Scottish strain of raspberry ringspot virus and is generally an inefficient vector of the English strain of raspberry ringspot virus. This is the only reported virus and nematode vector association where there may be some specificity in the dissociation of a virus strain within a nematode vector (Taylor and Brown, 1981).

Longidorus macroteromucronatus (Fig. 7):

Altherr (1974) described L. macroteromucronatus, from one female specimen obtained from East Germany but Sturhan (in litt.) considered that the specimen is probably identical to L. macrosoma. No other specimens of the species have been recorded.

Longidorus paraelongatus (Fig. 7)

This species, as with L. macroteromucronatus, was originally reported from East Germany and subsequently Sturhan (in litt.) has identified specimens of this species from forest nursery soils near Munster, West Germany.

Longidorus pisi (Fig. 8):

Schuurmans Stekhoven (1951) based the description of X. brevicaudatum on a larval specimen and Thorne (1961) transferred the species to the genus Longidorus. Aboul-Eid (1970) proposed that the X. brevicaudatum described by Siddiqi (1959) be considered a new species, which he transferred to the genus Longidorus and called L. siddiqii. Khan (1978) subsequently proposed L. siddiqii as a junior synonym of L. pisi Edward et al., 1964 and also that L. pisi and X. sandellum Heyns, 1966 should be used to describe a new genus. The two species proposed for the new genus can be distinguished from other Longidorus and Xiphinema spp. in having anteriorly located guide rings (similar to Longiorus spp.) and weakly developed basal flanges on their odontophores (most similar to Xiphinema spp.). The new genus was not named by Khan (1978) therefore the generic nomenclature of L. pisi, at present, remains unaltered. All reports of L. siddiqii and X. brevicaudatum from Europe are referred to L. pisi.

In Europe L. pisi has been reported from five countries four of

which are southern Mediterranean countries namely Cyprus, Egypt, Israel and Jordan. The species has also been reported from several biotopes in Bulgaria (Choleva-Abadzhieva, 1975). L. pisi is mainly a tropical to sub-tropical species occurring in India, South Africa and east and west Africa which probably accounts for its distribution being restricted to the southern part of Europe. A male L. pisi has been described from a population from Malawi, East Africa and morphometric differences between populations from Africa and India have been noted (Brown et al., 1982).

Longidorus poessneckensis (Fig. 7)

L. poessneckensis, which has been reported from only East Germany, has a rounded lip region and although resembling L. macrosoma is probably a separate species (Sturhan, in litt.).

Longidorus profundorum (Fig. 9):

L. profundorum has been recorded most frequently from Belgium, southern England, France and Spain, and occasionally from Wales, the Netherlands, West Germany, East Germany and Northern Ireland. In southern England L. profundorum has a distribution somewhat similar to that of L. macrosoma and in France the species is most frequently identified from soils from natural habitats and may be more widespread in France than is shown in Fig. 9. A population of L. profundorum in The Netherlands differed morphologically from type specimens and may belong to the L. goodeyi group of populations from The Netherlands but as yet has not been described as a separate species (Seinhorst and van Hoof, 1982). Fritzsche and Kegler (1968) reported L. profundorum to be a vector of a strain of raspberry ringspot virus but Trudgill et al. (1983) suggest that L. profundorum is probably not a virus vector species.

Longidorus protae (Fig. 4):

Prota et al. (1971) reported L. attenuatus present in soil collected from the rhizosphere of grapevine in northwest Sardinia. These specimens are now referred to L. protae (Lamberti and Bleve-Zacheo, 1977) and this species has not been reported from any other location in Europe.

Longidorus pseudoelongatus (Fig. 8)

This species has been recorded only in West Germany (Altherr, 1976) and the type specimen, which is in poor condition, appears similar to L. closelongatus (Sturhan, in litt.).

Longidorus sylphus (Fig. 7).

Choleva et al. (1980) reported the occurrence of L. sylphus in orchard and nursery (Rosa damascena) soils in several districts of Bulgaria. However, this report is considered an identification inquirenda as L. sylphus was originally described by Thorne (1939) as a rare species from forest soil, Wasatch Mountains, Utah, USA.

Longidorus taniwha (Fig. 9):

L. taniwha was originally described from New Zealand and has subsequently been recorded in southern France, Egypt and Israel. It is a relatively rare species in Europe and has most frequently been found in Egypt (Tarjan, 1964a; Oteifa and Tarjan, 1965).

Longidorus tarjani (Fig. 9):

L. tarjani has been identified from only two localities near d'Agde in southern France.

Longidorus vineacola (Fig. 9):

This species has a sporadic distribution in Europe usually being present in a country as a few isolated populations. However, in

northern West Germany, southern Netherlands and southern Israel several populations were found occurring in relatively small areas. In Israel L. vineacola has been reported causing much damage to onion (Allium sp.) crops (Cohn and Krikun, 1966). The species was originally described from grapevine from Trier, West Germany (Sturhan and Weischer, 1964). Subequently several of the populations identified from other countries have been found to have morphological and morphometrical differences when compared with the type specimens. A population of L. vineacola from Belgium was smaller in most respects when compared with type specimens (Aboul-Eid, 1970); Seinhorst (in litt.) observed a population in The Netherlands to have longer odontostyles, shorter distances from the anterior to guide ring and larger widths at the lip region than the type specimens; L. vineacola from northwest England had longer odontophores and shorter distances from the anterior to the guide ring than the type specimens and a population of L. vineacola from the Western Isles of Scotland had somewhat similar morphometrical differences when compared with the type specimens.

Terlidou (1967) reported a Longidorus sp. from Greece, present as a few individuals in soils from Lalioti in Corinth, Avlotes in Corfu, Lycovrysi in Attika and as a large population, including males and juveniles, from Varis in Rhodes. Drawings and photomicrographs are presented for the species but no morphometrics are given. Morphometrics calculated from the drawings, and the general appearance of the specimens in the photomicrographs appear to agree with those of L. vineacola. Therefore, the Longidorus sp. reported by Terlidou (1967) is identified as probably being L. vineacola but specimens from these locations should be examined to confirm the identification.

In virus transmission tests artichoke Italian latent virus was not transmitted by a population of L. vineacola from northwest England

(Brown, unpublished results).

II : 3 : 7 : 1 European Longidorus species inquirendae

Longidorus meyli

Meyl (1954) identified one female and one fourth stage larvae from Italy as Siddiqia maximus but Sturhan (1963a) described these specimens as L. meyli. Susequently Siddiqi (1965) noted that L. meyli was similar to L. vineacola and Aboul-Eid (1970) when comparing L. meyli and L. vineacola concluded that it was difficult to assume that L. meyli and L. vineacola were identical and therefore L. meyli should be considered a species inquirenda. However, as more information is now available concerning the variability between populations of L. vineacola it is possible that L. meyli represents an aberrant population of L. vineacola sensu lato. Also, it is possible that L. vineacola represents a species complex and further study may lead to the descriptions of several new species.

II : 3 : 8 The European distribution of Paralongidorus species.

Paralongidorus georgiensis (Fig. 10)

Siddiqi et al., (1963) erected the genus Paralongidorus and subsequently Khan et al., (1978) assigned some of the specimens accommodated in Paralongidorus to their newly erected genus Siddiqia. But, of the species remaining in the genus Paralongidorus, several appeared to more closely fulfill the criteria required for the genus Siddiqia than the genus Paralongidorus. One such species is P. georgiensis. However, the generic and specific nomenclature given by Khan et al., (1978) is used in this study. Therefore, P. georgiensis is the only representative of the genus Paralongidorus reported from Europe. The species has been identified only in soils from the Nile Delta, Egypt.

II : 3 : 9 The European distribution of Siddiqia species.

Siddiqia epimikis (Fig. 10):

The only record of the occurrence of this species is its original description from soil in Algeria (Dalmasso, 1969).

Siddiqia maximus (Fig. 10):

Dalmasso (1970) notes that S. maximus has a somewhat sporadic distribution similar to that of L. vineacola. However, S. maximus has been identified relatively frequently in soils from southern West Germany and from sandy alluvial soil in two areas in western France. It is likely that it is distributed throughout Europe as populations of S. maximus have been identified from Algeria, Greece, Portugal, Poland and eastern Scotland. In Britain S. maximus was probably introduced with planting material from Europe as it has been found only in private gardens, a forest nursery and a market garden. Little morphometric variability was recorded between populations examined from several European countries (McElroy et al., 1977). A population of S. maximus was tested as a potential virus vector and 17 of 20 viruses used in the study were not transmitted. Three viruses, raspberry ringspot, arabis mosaic and strawberry latent ringspot were transmitted only under experimental conditions and the authors conclude that S. maximus probably is not a natural virus vector species (McElroy et al., 1977).

Siddiqia remeyi (Fig. 10):

Altherr (1963) described S. remeyi from specimens recovered from northeastern France. It has not subsequently been identified from any other locality.

II : 3 : 10 The European distribution of Xiphinema species.

Xiphinema algeriense (Fig. 12):

X. algeriense has been identified only from the rhizosphere of grapevine near Mostaganem, Algeria. The presence of a combination of rare or exceptional characters for the Xiphinema genus namely, presence of a Z-organ, long and thin body, cephalated labial area, narrow amphidial aperture, post labial incisure and reduced basal flanges on the odontophore suggest that X. algeriense represents a transitional species towards Longidorus and other closely related genera (Luc and Kostadinov, 1981).

Xiphinema americanum (Fig. 11):

The species X. americanum has been investigated by several authors and the following is a summary of the current taxonomic status of the species.

X. americanum, the type species for the genus Xiphinema, was originally described by Cobb (1913) who gave only a brief species description together with the figure of the head and tail region of a male specimen. Later Cobb (1915) published a figure of an adult female which is presumed to be the same species. Further descriptions of X. americanum, from other populations were subsequently published by Imamura (1931), Thorne (1939), Loos (1949) and Carvalho (1955); Tarjan (1956) redescribed the species using male and female specimens. Because Cobb's original material was no longer available Tarjan (1958) designated a male specimen as the neotype.

In 1965 Lima presented, in his Ph.D. thesis, the results of a morphometric examination of specimens from several populations of X. americanum from several different countries and continents. He concluded that X. americanum was a species complex comprising seven species, four of which he described as new species. In a similar but separate study Tarjan (1969) also concluded that X. americanum was a species group comprising four closely related species, one species of which was X. mediterraneum which Lima (1965) had originally described.

Martelli and Lamberti (1967) described populations of X. mediterraneum based on Lima's (1965) description of the species. However, Coomans and Loof (1969) clarified the taxonomic position of X. mediterraneum and attributed Martelli and Lamberti (1967) as the original authors of the species because Lima's description was in his Ph.D. thesis, which could not be regarded as a publication under the rules of the Regles Internationales de la Nomenclature Zoologique. Later, X. mediterraneum was made a junior synonym of X. pachtaicum (Tulaganov, 1938) Kiryanova, 1951 (Siddiqi and Lamberti, 1977).

Cohn and Sher (1972) proposed the erection of several sub-genera within the genus Xiphinema. This proposal was rejected by Luc and Dalmasso (1975) as the sub-genera proposed by Cohn and Sher (1972) were based upon characters which did not appear to have distinguishable evolutionary bases. Luc and Dalmasso (1975) suggested that Xiphinema species could be placed into groups using several taxonomic and morphological characters but that these groups were not considered to be sub-genera. Meanwhile, Heyns (1974a) described the X. americanum group of species from South Africa and concluded that demarcation of species within the X. americanum group was problematical and unsatisfactory but that several of the species proposed by Lima (1965) appeared to be justified. Lamberti and Bleve-Zacheo (1979) studied X. americanum sensu lato and concluded that the denomination X. americanum sensu lato need no longer be retained. They recognised 25 species, 15 of them new, which could be sub-divided into six groups of species. According to Lamberti and Bleve-Zacheo (1979) X. americanum sensu stricto would now be recognised as having a limited distribution in the eastern part of the North American continent and that most records of X. americanum reported from European countries are now referred to X. pachtaicum. However, some records of X. americanum from Europe are referred to

other Xiphinema spp. (Lamberti and Bleve-Zacheo, 1979). In the present study of the distribution of Longidoroidea in Europe it has been assumed that all records of X. americanum in Europe refer to X. pachtaicum except for a few cases where X. americanum has been synonomised with other Xiphinema spp. (details are given under the appropriate Xiphinema spp. headings).

X. americanum and X. pachtaicum recently have both been identified from soils in Yugoslavia and the morphometrics presented for both species readily identifies the occurrence of two Xiphinema species (Hrzic, 1978). However, the morphometrics presented for X. americanum allow the species to be identified as possibly being one of several species in the X. americanum species group including X. brevicolle and X. rivesi both of which are known to occur in Europe. Therefore, it is concluded that until further information is made available concerning the X. americanum specimens from Yugoslavia the report of this species should be considered as an identification inquirenda.

In the USA X. americanum has been reported to transmit tomato ringspot, tobacco ringspot, peach rosette mosaic and cherry rasp leaf viruses, although probably X. californicum, as well as or rather than X. americanum, should now be recognised as a vector of these viruses (Taylor and Brown, 1981). The viruses have been reported from Europe only as being intercepted in or having been recently imported in planting material. However, Martelli (1975, 1978) reports that tomato ringspot virus might possibly be established in grapevines growing in Yugoslavia. If this report were confirmed and X. americanum, reported by Hrzic (1978), is found associated with the virus in the Yugoslavian vineyard this would be the first recorded occurrence of a North American nepovirus and vector combination in Europe.

Xiphinema basilgoodeyi (Fig. 11):

The occurrence of X. basilgoodeyi, a mainly tropical species, in Europe has been reported once from Yugoslavia (Hrzic, 1978). However, the morphometrics presented for the Yugoslavian specimens allow the specimens to be identified as being one of several other Xiphinema spp. present in Europe e.g. X. index, X. neovuittenezi and X. vuittenezi. Therefore this report of X. basilgoodeyi should be considered an identification inquirenda until authenticity can be confirmed.

Xiphinema brevicolle (Fig. 12):

X. brevicolle has a sporadic, widespread, distribution in Europe, ranging from West Germany in the north and Israel in the south, Portugal in the west and Czechoslovakia in the east. The species has most frequently been identified in soils from Israel, Spain and Italy. Szczygiel et al., (1969) reported X americanum from eastern Poland but later Szczgiel (1974) amended the original identification to X. brevicolle and Lamberti and Bleve-Zacheo (1979) confirmed the correction.

In laboratory experiments X. brevicolle has been implicated as a vector of tomato ringspot virus (Fritzsche and Kegler, 1968) but Trudgill et al., 1983) considered that the published evidence was inconclusive.

Xiphinema clavatum (Fig. 12):

X. clavatum has been identified only once from Europe where it was associated with grapevines in central Italy (Roca and Lamberti, 1978).

Xiphinema coxi (Fig. 12):

X. coxi is recognised as being a species complex comprising at least three distinguishable forms. Dalmasso (1970) recognised the presence of two forms from Europe which were obviously different from

the type population described from Florida, USA (Tarjan, 1964b). The European populations could be further differentiated, as specimens from Brittany, France were smaller (L less than 3 mm) than those from eastern France. Taylor and Brown (1976) also found that English populations of X. coxi had shorter odontostyles and odontophores, smaller c' ratios and more apophyses present in the Z organ than type specimens from Florida. In West Germany two forms of X. coxi appear to exist (Sturhan, in litt.) with one form similar to the type Florida population. The second form has a smaller body and stylet length than the type population also a Z organ similar to X. diversicaudatum and is probably similar to the English populations. A third form with a Z organ similar to X. diversicaudatum but morphologically intermediate between the other two types has been identified from Portugal, Madeira and the Azores (Sturhan, in litt.). It is likely therefore that the X. coxi species complex will be divided into X. coxi sensu stricto and two new species.

At present X. coxi sensu lato appears to have a sporadic distribution in countries in north and west Europe and seems to be associated with relatively undisturbed biotopes.

In experimental tests X. coxi has been implicated as a vector of brome mosaic virus (Schmidt et al., 1963), arabis mosaic virus (Fritzsche, 1964), cherry leaf roll virus (Fritzsche and Kegler, 1964), strawberry latent ringspot virus (Putz and Stocky, 1970) and tobacco ringspot virus (van Hoof, 1971). However, Trudgill et al., 1983 suggest that the evidence for virus transmission is inconclusive.

Xiphinema dentatum (Fig. 12):

Sturhan (1978) originally described X. dentatum from soil samples from central West Germany and it has not subsequently been reported from any other locality in Europe.

Xiphinema diversicaudatum (Fig. 12):

This species has been recorded from most European countries except Finland and Romania and the southern Mediterranean countries. Cohn (1969) identified X. diversicaudatum from several biotopes in Israel but re-examination of these specimens showed that they were morphologically smaller than X. diversicaudatum and the female genital tracts did not contain a Z differentiation. These specimens have been described as new species, Xiphinema Israeliae (Luc et al., 1981; see IV : 1:1). Also, X. paraelongatum Altherr, 1958 is now recognised as a junior synonym of X. diversicaudatum (Luc and Tarjan, 1963).

X. diversicaudatum was the first European longidoroid nematode to be reported as a virus vector (Jha and Posnette, 1959; Harrison and Cadman, 1959). It was found in Britain in association with a range of crop species infected with arabis mosaic and strawberry latent ringspot viruses and in laboratory experiments was shown to be a vector of them (Jha and Posnette, 1959; Harrison and Cadman, 1959; Lister, 1964). Later X. diversicaudatum was reported as a vector of brome mosaic, cherry leafroll and carnation ringspot viruses (Schmidt et al., 1963; Fritzsche and Kegler, 1964; Fritzsche and Schmelzer, 1967), but Trudgill et al., (1983) consider the experimental evidence for transmission of these viruses to be inconclusive.

(NOTE: More information concerning the distribution, morphology, taxonomy and biology of X. diversicaudatum and its ability to transmit viruses is presented in Chapters IV to X inclusive).

Xiphinema elongatum (Fig. 13):

X. elongatum has been recorded from several tropical and sub-tropical countries throughout the world. The mainly tropical and sub-tropical distribution of this species is reflected in its European distribution as it has only been recorded from three southern Mediterranean countries namely, Algeria, Egypt and Israel.

Xiphinema ensiculiferum (Fig. 11):

Cohn and Sher (1972) in reviewing the genus Xiphinema and proposing several new sub-genera, record morphometrics of a population of X. ensiculiferum from Israel. This is the only report of the presence of this mainly tropical species in Europe.

Xiphinema globosum (Fig. 13):

Sturhan (1978) originally described this species from several biotopes in Bavaria, West Germany and it has not been identified elsewhere in Europe.

Xiphinema index (Fig. 13):

Southey (1973) reported this species from Iran where it has been identified in soils from the rhizosphere of natural woodlands and wild grapevines (Sturhan in Weischer, 1975; Mojtahedi et al. (1980). It is now generally accepted that X. index originated in the Middle East and has been distributed from there to most grapevine growing areas of the world in soil accompanying vines used for propagation. X. index has been reported from most areas of Europe where grapevines are grown but in central Europe it is replaced by X. vuittenezi which is more frequently associated with soils from vineyards. However, X. index may be present in many vineyards in central Europe as very small populations which might easily escape detection by routine soil sampling (see X. vuittenezi).

In vineyards in Corsica X. index is rare and Dalmasso (1970) suggests this might be due to the insularity and peculiarities of Corsican vineyards. Also, in Britain where the Romans established many vineyards and where, in the past decade, about 500 ha of new commercial vineyards have been planted, X. index has not been identified during extensive soil sampling (Taylor and Brown, 1976;

1982). However, X. index populations have been maintained successfully in unheated glasshouses in southern England (Brown and Taylor, 1977) and therefore environmental conditions would not appear to be a factor preventing the establishment of this species in Britain.

X. index is generally considered to feed at root tips (Cohn, 1975) but in feeding studies in Israel Cohn (1970) recorded X. index feeding mostly along the roots, only occasionally near the root tips. In California, USA X. index females fed exclusively at the root tips whereas the larval stages, particularly the younger stages, also fed on the piliferous region of the root system (Fisher and Raski, 1967). It is suspected that differences exist between populations of X. index in their ability to transmit grapevine fanleaf virus (Taylor and Brown, 1982). The differences observed in feeding behaviour between populations might, in part, account for differences in abilities of populations to transmit virus.

In natural conditions X. index appears to be a host specific parasite and is associated almost exclusively with grapevine and fig (Ficus carica). But, occasionally it has been identified from soils collected from the rhizosphere of other plant species. Siddiqi (1974), in a redescription of the species, records more than 30 plant species reported to be hosts for the nematode. In laboratory studies tomato (Lycopersicon esculentum) cv Moneymaker was found to be a host for X. index from populations from France, Israel, Italy and the USA but tomato cv Haubners Vollendung was a host for nematodes from only the French and USA populations (Coiro and Brown, 1983). Some physiological differences have also been reported to occur between populations of X. index. The life cycle of X. index in California, USA was completed in 22 to 27 days at 24 C, In Israel the life cycle

was completed in 7 to 9 months at 20 to 23 C and 3 to 5 months at 28 C. In Sardinia 1 year was required although in glasshouse studies in Italy only 2 to 4 months at 20 to 22 C were required (Radewald and Raski, 1962; Cohn and Mordechai, 1969; Prota and Garau, 1973; Prota et al., 1977). Coiro and Brown (1983) reported that in laboratory studies X. index from populations from France, Israel, Italy and the USA completed their life cycles in less than 12 wk at 18 C under fig but took longer than 12 wk under strawberry.

X. index was the first nematode to be proven to be a virus vector (Hewitt et al., 1958) and grapevine fanleaf virus and its vector X. index have been reported from most grapevine growing areas of the world including Europe. Mali et al., (1975) reported X. index as a vector of grapevine chrome mosaic virus but Trudgill et al. (1983) suggest that the published evidence for this association is inconclusive. Also, rikettsia-like organisms, apparently causing yellows disease of grapevine in West Germany, have been reported to be transmitted by X. index (Rumbos et al., 1977). However, existing hypotheses concerning specificity between viruses and their nematode vectors (Taylor and Brown, 1981) would suggest that this latter association is unlikely.

Xiphinema ingens (Fig. 13):

In Europe X. ingens has been reported only from five countries - Israel, where it has been identified from several localities; Italy, where it appears to comprise a species complex making identification difficult (Lamberti, in litt.); Spain, where it is also present at several localities including the northwest of the country; in Jordan and Turkey where it is relatively rare. An intersex female with well developed male characteristics was identified from a population of X. ingens from soil around olive at Melilli, Siracusa, Italy (Lamberti et al., 1975).

Xiphinema insigne (Fig. 14):

X. insigne has been reported from only three countries in Europe at the eastern end of the Mediterranean namely, Egypt, Israel and Jordan. It has been recorded from several locations in each country in association with a range of crop plants.

Xiphinema israeliae (Fig. 12);

During a survey of longidoroid nematodes in Israel, carried out during the mid 1960's, X. diversicaudatum was identified in 13 of 32 soil samples from citrus, 3 of 10 soil samples from avocado (Persea gratissima), 2 of 26 soil samples from grapevine and occasionally from soils associated with Rosa sp. However, after re-examination of these specimens they have been referred to X. israeliae (Luc et al., 1982) which has so far been identified only from Israel.

Xiphinema italiae (Fig. 11):

Meyl (1953) originally described X. italiae but Luc and Tarjan (1963) designated X. italiae as a species inquirendae because the type material was lost and the original descriptions had, in part, been based upon juvenile stages. Martelli et al., (1966) resurrected the species, designated a neotype from the original type location and made X. arenarium Luc and Dalmasso, 1963 a junior synonym. Meanwhile Stoyanov (1964) and Siddiqi (1964) had described X. bulgariense and X. conurum respectively as new species but Cohn and Sher (1972) made both these species junior synonyms of X. italiae. Therefore, all records of X. arenarium, X. bulgariense and X. conurum in Europe are referred to X. italiae in this study. But, further specimens of X. conurum subsequently obtained from Tunisia have been found to be sufficiently morphologically different from X. italiae to perhaps allow the specific status of X. conurum to be eventually re-established (Dalmasso, pers. comm.).

X. italiae has been reported to occur in 12 European countries, most frequently in countries abutting the Mediterranean sea. It commonly occurs in soils along the coastal regions of these countries and in France it is morphologically smaller in localities where there are large fractions of silt and clay (Dalmasso, 1970). X. italiae has also been identified in soil samples from the Atlantic seaboard of Portugal and Spain, the coastal region of Rumania and is distributed throughout Bulgaria. Cohn et al., (1970) reported X. italiae to be a vector of grapevine fanleaf virus in Israel but no further experiments have been done to confirm this report except that by Martelli (1975) who completed one experiment in which X. italiae appeared to transmit grapevine fanleaf virus in one replicate. Evidence of virus transmission by X. italiae occurring in field situations is not readily available (Taylor and Brown, 1981, 1982) therefore some doubt has been expressed about the ability of this nematode to transmit virus (Trudgill et al., 1983).

Xiphinema neovuittenezi (Fig. 11):

This species has a sporadic distribution in Europe having been identified from only a few soil samples in Bulgaria, Spain, Yugoslavia and from France, from where it was originally described (Dalmasso, 1970). Stegarescu (1977) proposed that although X. neovuittenezi is a bisexual species and X. vuittenezi is a parthenogenetic species they differ in only small morphometric details and therefore X. neovuittenezi should be made a junior synonym of X. vuittenezi. However, this proposal was published as an abstract and until further details are presented it has not been accepted in this study.

Xiphinema pachtaicum (Fig. 14):

This species is the most widespread Xiphinema species and the most frequently identified in Mediterranean countries. It has also

been reported from localities in several non-Mediterranean countries: southern England, central West Germany, Portugal, Switzerland, Hungary and Bulgaria. Also, X. pachtaicum has been identified from soils from glasshouses near Oslo, Norway where it probably was introduced with propagating material (Stoen, M., in litt.). Szczygiel et al. (1969) reported X. americanum from Poland but the specimens were later referred to X. brevicolle (Szczygiel, 1974). Wasilewska (1971) also reported X. pachtaicum (= X. americanum; for nomenclatorial information regarding X. pachtaicum in Europe see X. americanum) from Poland and although this record of X. pachtaicum in Poland is used in this study it is regarded as probably being an identification inquirenda . In Italy X. pachtaicum probably represents a species complex and species identification is difficult (Lamberti, F., pers. comm.).

Like X. index, X. pachtaicum has been reported from several countries outside Europe including California, USA and was probably introduced to these countries with propagating material. X. pachtaicum tolerates drought conditions and is most frequently identified from soil with a large clay content. Dalmasso (1970) reports that in France X. pachtaicum is rarely found in sandy, wet or poorly aerated soils whereas in Israel the nematode is prevalent in such soils (Cohn, 1969).

Most of the published reports of X. pachtaicum refer only to its occurrence , location and / or association with particular plant species. Little or no information is available regarding its biology or pathogenicity on crop plants. Attempts to culture X. pachtaicum in the laboratory or glasshouse have failed and in some cases this may be due to microsporidians (Bacillidium, fam. Mrazekiidae) parasitizing the female nematodes gonads (Morone De Lucia and Grimaldi De Zio, 1973). Adams and Eichermuller (1963, 1964) reported similar

infections in X. americanum. Most populations of X. americanum from western Virginia, USA were naturally infected with the bacterium Pseudomonas denitrificans. Larval stages were infected throughout the body except the oesophagus, and in adult females the infection was concentrated in the intestine and the ovaries. Siddiqi (1973) observed similar bacteria in the ovarial cells of X. americanum from Rhode Island, USA and western Australia but specimens from India were not infected (these last probably now refer to a different species, see Lamberti and Bleve-Zacheo, 1979). Bacteria have also been found in other Xiphinema spp. e.g. in the ovaries and intestines of females and the intestines of juvenile X. silvaticum, from different populations, from Mauritius (Luc and Williams, 1978).

In Italy X. pachtaicum was identified from the rhizosphere of peach trees infected with "stem pitting" disease and in grapevines affected by grapevine fanleaf virus(Guinchedi and Tacconi, 1974; Alfara Garcia, 1971). However, there is so far no experimental evidence of its being a vector of the viruses.

Xiphinema pini (Fig. 14):

This species has only been reported from southern Israel where it has a relatively restricted distribution.

Xiphinema pyrenaicum (Fig. 11):

Dalmasso (1970) originally described X. pyrenaicum from western and southwest France and subsequently Arias (1979) identified the species from soil from northwest Spain.

Xiphinema rivesi (Fig. 14):

Dalmasso (1969) originally described X. rivesi from several localities in western France and it has subsequently been recorded from central Spain and West Germany and from Guadeloupe in the Caribbean (Arias and Navacerrada, 1973; A. Dalmasso, pers. comm.;

D.Sturhan, in litt.). In historical times ships sailed from Brittany, France to the French West Indian colonies and therefore X. rivesi may have been introduced to France from the West Indies (Dalmasso, pers. comm.). X. rivesi is tentatively placed in the X. americanum group of species but differs from all species in the group by having a lip region continuous with the rest of the body. Lamberti and Bleve-Zacheo (1979) reported X. rivesi populations from Nebraska and Kansas, USA which were the first extra-European records of the species. However, X. rivesi has now been reported in 42 of 66 soil samples examined from seven counties of Pennsylvania, USA; X. americanum was also present in 12 of 33 samples containing X. rivesi (Forer, 1981). Also Forer and Stouffer (1981) reported X. rivesi as a vector of tomato ringspot virus in Pennsylvania but no experimental details were given in the report which was an abstract. There is no information of the association of X. rivesi with any virus in Europe and tomato ringspot virus is not known to be present except perhaps in Yugoslavia (Martelli, 1975, 1978).

Xiphinema rotundatum (Fig. 11):

Andrassy (1973) reported X. rotundatum from Hungary and Hrzic (1978) reported it from Yugoslavia but these are considered to be identifications inquirenda until the identifications can be confirmed.

X. rotundatum is one of a group of seven Xiphinema species, mainly reported from Africa, which have true Z organs, containing a small number of refringent "teeth", present in the female genital tracts (Luc and Dalmasso, 1975).

Xiphinema sahelense (Fig. 14).

X. sahelense was originally described from specimens extracted from soil collected from the rhizosphere of grapevines in Algeria.

X. amarantum was decribed from the Iberian peninsula but subsequently was made a junior synonym of X. sahelense (Macara, 1970, 1972).

Xiphinema turcicum (Fig. 14):

In Europe X. turcicum appears to have a sporadic distribution. It usually occurs as discrete, isolated populations although in central Spain several populations have been reported from a relatively small area. Dalmasso (1969) reported that a population of X. turcicum from Algeria differed from the type specimens in the stucture of the gonads, the sphinctre at the Z organ and in smaller body and spear lengths. Also, morphological differences between three populations of X. turcicum examined by D. Sturhan (in litt.) may be sufficient to warrant the erection of new species. In Algeria grapevine fanleaf virus was found to be spreading in a vineyard in which X. turcicum was present but X. index was not identified (C. Scotto La Massesse, in litt.). However laboratory experiments have not been done to study this association and it is possible that a similar situation exists as with X. vuittenezi and grapevine fanleaf virus in a vineyard in Switzerland (see X. vuittenezi).

Xiphinema vuittenezi (Fig. 11):

In central Europe this species is relatively common, particularly in vineyards where it replaces X. index and X. italiae as being the most frequently identified species. Also in Poland X. vuittenezi is the most frequently recorded Xiphinema species (M.W. Brzeski in Dalmasso, 1970). Although central Europe appears to be the main distribution area for X. vuittenezi it has also been identified in soils from as far north as Yorkshire in northern England; southwest Portugal and in the Jordan Valley in Jordan.

In Czechoslovakia, West Germany and France X. vuittenezi has been associated with grapevine fanleaf virus infected with grapevines but

experimental evidence does not support the suggestion of it being a virus vector (Taylor and Brown, 1981, 1982). In Switzerland X. vuittenezi was associated with the spread of grapevine fanleaf virus in a vineyard for several years but small numbers of X. index were subsequently identified from the same soil (J. Klinger, in litt.). This latter species is well documented as being a vector of grapevine fanleaf virus therefore X. vuittenezi is not considered to be a virus vector species.

II : 3 : 10 : 1 European Xiphinema species inquirendae.

Two Xiphinema species inquirendae have been reported from biotopes in Europe. X. grande was originally described from specimens from Switzerland (Steiner, 1914) and also has been reported from Germany and Poland (Schneider, 1953; Wikowska, 1958). But, the specimen from Spain, identified as X. grande by Gadea (1955), refers to another Xiphinema species (Sturhan, 1963b). Thorne (1939) and Sturhan (1963b) considered it likely that X. grande was an Enchodelus sp. but that insufficient information was available to describe the species. Therefore, in lists of Xiphinema species (Luc and Tarjan, 1963; Cohn and Sher, 1972; Luc and Dalmasso, 1975) X. grande is included as a species inquirenda.

X. makrodorum was described from specimens from Czechoslovakia (Vanha, 1893) and placed in the Xiphinema genus by Thorne (1939). However, Thorne (1939) stated that "if Vanha's figure of the neck (of X. makrodorum) is correct this species probably represents an unknown genus". Luc and Tarjan (1963) considered X. makrodorum a species inquirendae because of its differences from other Xiphinema species and Cohn and Sher (1972) included it as a species inquirenda in their list of Xiphinema species but Luc and Dalmasso (1975) omitted it from their list of Xiphinema species. However, Luc and Dalmasso (1975)

included X. dolichodorum in their list of Xiphinema species as a species inquirendae but Thorne (1939) had synonomised this species with X. macrodorum . Therefore, X. macrodorum takes precedence as the specific name as it was used earlier than X. dolichodorum.

II : 4 DISCUSSION

Before Hewitt et al., (1958) reported X. index to be a vector of grapevine fanleaf virus only 22 members of the Longidoroidea had been described; subsequently a further 183 species were described from many different parts of the world. Of the 205 members of the Longidoroidea currently described 58 species (28%) have been reported from Europe, of which 29 are Longidorus spp., 25 are Xiphinema spp., 3 are Siddiqia spp., and 1 is a Paralongidorus sp. The number of species in the four genera of Longidoroidea reported from Europe, as percentages of the total number of species in each genus is 59% for Longidorus, 22% for Xiphinema, 18% for Siddiqia and 9% for Paralongidorus.

In Europe the genus Longidorus tends to have a predominantly northern European distribution whereas the genus Xiphinema has a more southerly distribution although several species e.g. X. dentatum, X. globosum, X. coxi, etc. are exceptions to this trend. The three Siddiqia species in Europe can be classified as northern European species and the one Paralongidorus species as a southern species. However, seven arbitrary geographical groupings of the Longidoroidea species present in Europe can be made from the more general northern and southern groupings of the four genera:

Northern:- L. attenuatus, L. caespiticola, L. cylindricaudatus, L. elongatus, L. globulicauda, L. goodeyi, L. intermedius, L. leptocephalus, L. macrosoma, L.paraelongatus, L. pseudoelongatus, S. maximus, S. remeyi, X. coxi, X. dentatum and X. globosum.

Southern:- L. apulus, L. closelongatus, L. fasciatus, L. juvenilis, L. protea, L. tarjani, X. americanum, X. basilgoodeyi, X. clavatum, X. ingens and X. neovuittenezi.

Western:- L. profundorum, X. pyrenaicum, X. rivesi and X. sahelense.

European:- L. vineacola, X. brevicolle, X. diversicaudatum, and X. vuittenezi.

Meditteranean:- L. laevicapitatus, L. taniwha, X. index, X. italiae, X. pachtaicum and X. turcicum.

Southern Mediterranean:- L. africanus, L. cohni, L. congoensis, L. pisi, S. epimikis, P. georgiensis, X. algeriense, X. elongatum, X. ensiculiferum, X. insigne, X. israeliae and X. pini.

This tentative arrangement of geographical groups of species may be useful, especially as an aid to the identification of the species by the extension worker. As the taxonomy of the Longidoroidea develops several of the existing species may be found to have more restricted or extended European distributions than at present, with a possible reclassification of the above groups.

From throughout the world 18 Longidorus species have been reported to act as vectors of plant viruses and 15 of these species and their associated viruses have been reported to occur in Europe. Similarly 24 Xiphinema species and plant virus associations have been reported and 16 of these species and their associated viruses have been reported to occur in Europe. These nematode and virus associations are reported to occur throughout Europe from the southern Mediterranean countries to northern Scotland and from eastern European countries to Spain and Portugal in the west. Therefore, the virus

vector nematode species cannot all be placed in one geographical distribution zone.

Several workers have tentatively discussed the distribution of Longidoroidea in relation to Palaeoecology (Dalmasso, 1970; McNamara and Flegg, 1981; Taylor and Brown, 1976; Rau, 1975) but much of these discussions must be speculative as there is little evidence to support the views put forward. It is therefore considered inappropriate to attempt to discuss the present distribution of European Longidoroidea except in relation to Neoecological factors. Nematodes are dependent on various factors which, combined, comprise the biotope in which they may survive and successfully reproduce to maintain a breeding population. But these factors, such as soil type, soil porosity, host plant, precipitation and temperature are interrelated. Hashim (1979) reported that the nematode fauna of the rain-fed, elevated areas of Jordan resembles that of Europe but that in the Jordan Valley and the Southern Ghors the nematode fauna is more similar to sub-tropical Africa. Also, Dalmasso (1970) reported that in France several members of the Longidoroidea appear to be dependent on the local climate e.g. X. neovuittenezi is found only in very warm regions with an annual rainfall of less than 500 mm., X. vuittenezi is found in areas with an annual rainfall between 500 and 700 mm but in surrounding areas which have larger annual rainfalls this species is absent. Therefore, in some areas of European countries the local climate (= microclimate) would appear to be correlated with the occurrence of particular nematode species. However, differences in the microclimate presumably also affect the local vegetation including arable plants, and plant hosts can be a major factor limiting the distribution of some nematode species e.g. in field situations X. index is usually found only associated with grapevine and fig (Cohn, 1975; Siddiqi, 1974). The complex inter-relationships between

microclimate, soil factors, plant species and nematode species are probably many and varied. It is unlikely therefore that an examination, even at the continental level, of any one factor in isolation from the others will offer any useful explanation of what determines the European distributions of the Longidoroidea.

Today man is probably the most important influence on the dissemination and resultant distribution of nematode species. Much evidence is readily available concerning the suspected and known involvement of man with the dissemination of nematode species (Taylor, 1977). Examples of longidoroids which have been widely disseminated include X. index which, with its associated virus grapevine fanleaf, has been disseminated throughout Europe and other grapevine growing areas of the world from ancient Persia, its area of origin (Hewitt, 1968). Taylor and Brown (1976) reported L. elongatus from several of the Scottish islands where it was found only in soils from private gardens or similar sites and thus was probably introduced to these biotopes with planting material. Direct evidence of man's involvement in distributing nematodes is illustrated by the interception and identification of nematodes on imported plants e.g. X. incognitum and X. insigne associated with coniferous and deciduous "bonsai" species and dwarf conifers respectively, imported into England (Southey and Aitkenhead, 1972); also X. hygrophilum was originally described from a tropical aquatic plant, Cryptocoryne sp., growing at the Royal Botanic Gardens, Kew, England (Southey and Luc, 1973).

Although man may be responsible for widely distributing nematodes with plant material and soil, the establishment of nematode populations in new areas is determined by many factors e.g. presence of suitable host plants, soil, climate. A clear definition of the taxonomy of European Longidoroidea and much more information about

their biology and ecology may allow some factors to be identified which have influenced and are influencing the continental distributions of some of these nematode species.

The taxonomy of the superfamily Longidoroidea and the species of which it is comprised is, as yet, not fully described in relation to European species. Although some existing species in Europe may be synonimised e.g. X. neovuittenezi and X. vuittenezi (Stegarescu, 1977), it seems likely that, as the taxonomy develops, further species will be described and reported to occur in Europe. Five Longidorus species complexes (a species complex consists of two or more morphologically distinguishable populations which are identified and referred to as comprising one species) have been reported from Europe - L. caespiticola, L. elongatus, L. goodeyi, L. profundorum and L. vineacola. L. leptocephalus may also be a species complex as it appears to have a large and small form although, morphometrically, these forms overlap. Also, five Xiphinema species complexes have been reported - X. coxi, X. diversicaudatum, X. index, X. pachtaicum and X. turcicum. Thus there are likely to be at least 10 or 11 more Longidoroidea reported to occur in Europe in addition to any as yet undiscovered or undescribed species in European countries which would further increase the number of species of the Longidoroidea superfamily reported from Europe - L. apulus, L. protae, L. fasciatus, L. intermedius, L. cylindricaudatus, X. algeriense, X. dentatum, X. globosum and X. israeliae are recently described species from Algeria, Italy, Greece, The Netherlands, West Germany and Israel although these countries have been relatively well surveyed for Longidoroidea in previous years.

The "morpho-species" (species described on the basis of morphological differences) is widely used in the systematics of

nematodes, including the Longidoroidea, because of the abundance of thelytokous species (from the Greek:thelys, female; tokos, offspring. Reproduction without fertilization by the male) to which the classical biological species concept (amphimictic species; interbreeding and gene interchange between individuals) cannot be applied. Recently, Dalmasso and Berge (1983) suggested that the taxonomy of nematodes could be based upon protein polymorphism, rather than morphology, an approach which they successfully applied to differentiate Meloidogyne spp. They also described a hypothetical model explaining the evolution in Longidoroidea in which populations of ancestral amphimictic forms (species) may be affected by inbreeding resulting in complete homozygosity, subsequent facultative meiotic parthenogenesis with a resulting loss of males, and finally mutations giving rise to "clonal species". These clonal species would be morphologically/anatomically similar within species complexes and groups of species e.g. L. elongatus complex, X. americanum group. However, an examination based on published descriptions of Xiphinema spp. present in Europe and of Longidorus spp., in relation to the species morphological/anatomical similarities , geographical distributions and probable methods of reproduction may give a better insight into the potential for specific groups and their possible composition. Using these data and applying the model of Dalmasso and Berge (1983), for evolution in Longidoroidea, tentative specific groups of Longidorus and Xiphinema have been erected (Tabs. 5 and 6).

Luc (1979) erected four main morphological/anatomical groups of Xiphinema species which were further sub-divided into 12 sub-groups of species. These groups and sub-groups of Xiphinema species were abridged and adapted, with the inclusion of geographical data, to give the results presented in Table 6. Similarities in the general shape of the anterior regions between Longidorus species were used to erect

four main groups of species, and in one instance, group A, the absence and presence of basal lobes with the amphidial pouch were used to sub-divide this category. Geographical data were used, as with the groups of Xiphinema species, to further sub-divide the specific Longidorus groups (Tab. 5).

The data obtained from published reports and presented in Tables 5 and 6 appear to suggest possible geographical origins, at the continental level, of Longidorus and some Xiphinema species. Furthermore, groups of morphologically/anatomically similiar Xiphinema species which occur in Europe and in the Longidorus genus generally comprise an amphimictic (ancestral) species and several thelytokous (clonal) species. The specific composition of these groups of species would seem to support the model of evolution in the Longidoroidea suggested by Dalmasso and Berge (1983). These groupings of Longidorus and Xiphinema species are tentative and other morphological/anatomical characters of equal or more pertinent evolutionary significance may be used to create other groupings of species. Also, as the taxonomy of the Longidoroidea develops with the descriptions of further morpho-species it is probable that the specific groups given in Tables 5 and 6 will have to be restructured. The specific groups of Longidorus and Xiphinema presented here although perhaps of some value to the study of the systematics of the Longidoroidea cannot be referred to sub-genera. Only a thorough revision of the taxonomy of the Longidoroidea probably including an examination of protein polymorphism within the superfamily, as suggested by Dalmasso and Berge (1983), will help establish valid evolutionary specific groups which in turn may give rise to valid subgeneric status to some groups.

II : 5 CONCLUSIONS

A) Longidoroid nematodes are widespread and occur in almost all European countries. Fifty-eight species comprising 29 Longidorus, 25 Xiphinema, 3 Siddiqia and 1 Paralongidorus species have been recorded from Europe, of which 9 Longidorus and 8 Xiphinema species have been reported to be vectors of plant viruses.

B) Generally the genus Longidorus tends to have a predominantly northern European distribution whereas the genus Xiphinema has a more southerly distribution.

C) In Europe the continental distribution patterns of Longidoroidea superfamily species do not each appear to be related with any one ecological factor e.g. soil type, evapo-transpiration, altitude, etc. The ecological factors which comprise a biotope in which a population of a nematode species successfully exists form complex inter-relationships with one another. Thus it may be difficult to separate and identify those factors which directly affect the nematodes from those which cause an effect through second, and perhaps subsequent, factors.

D) Much evidence is available concerning the influence of man on the dissemination and resultant distribution of longidoroid nematodes in Europe.

E) The taxonomy of the Longidoroidea superfamily and the species of which it is comprised is not fully described in relation to European species. Several species complexes are reported to occur in Europe, thus, there are likely to be 10 or 11 more Longidoroidea superfamily species reported to occur in Europe in addition to any as yet undiscovered or undescribed species which may exist in Europe.

F) Groups of morphologically/anatomically similar Xiphinema

species which occur in Europe and in the nematodes Longidorus genus generally comprise an amphimictic and several thelytokous species. The specific composition of these groups supports a model of evolution in the Longidoroidea in which the amphimictic species is the "ancestral form" and the thelytokous species are "clonal forms" which have evolved from the amphimictic (ancestral) species.

TABLE 1 : Longidorus Micoletzky, 1922 species present in European countries.

L. africanus	Merny, 1966
L. apulus *+	Lamberti and Bleve-Zacheo, 1977
L. attenuatus *+	Hooper, 1961
L. caespiticola *	Hooper, 1961
L. closelongatus	Stoyanov, 1964
L. cohni	Heyns, 1969
L. congoensis	Aboul-Eid, 1970
L. cylindricaudatus	Kozlowska and Seinhorst, 1979
L. elongatus *+	(de Man, 1876) Thorne and Swanger, 1936
L. euonymus *	Mali and Hooper, 1974
L. fasciatus *	Roca and Lamberti, 1981
L. globulicauda	Dalmasso, 1969
L. goodeyi	Hooper, 1961
L. intermedius	Kozlowska and Seinhorst, 1979
L. juvenilis	Dalmasso, 1969
L. laevicapitatus	Williams, 1959
L. leptocephalus *	Hooper, 1961
L. macrosoma *+	Hooper, 1961
L. macroteromucronatus	Altherr, 1974
L. paraelongatus	Altherr, 1974
L. pisi	Edward et al, 1964
L. poessneckensis	Altherr, 1974
L. profundorum *	Hooper, 1966
L. protae	Lamberti and Bleve-Zacheo, 1977
L. pseudoelongatus	Altherr, 1976
L. sylphus	Thorne, 1939
L. taniwha	Clark, 1963
L. tarjani	Siddiqi, 1962
L. vineacola	Sturhan and Weischer, 1964

Species Inquirendae

L. meyli	Sturhan, 1963a

* species reported transmitting virus
\+ species accepted as virus vectors by Trudgill et al. (1983)

TABLE 2 : Xiphinema Cobb, 1913, Siddiqia Khan, Chawla and Saha, 1978 and Paralongidorus Siddiqi, Hooper and Khan, 1963 species present in European countries.

X. algeriense	Luc and Kostadinov, 1981
X. americanum *+	Cobb, 1913
X. basilgoodeyi	Coomans, 1964
X. brevicolle *	Lordello and Da Costa, 1961
X. clavatum	Heyns, 1965
X. coxi *	Tarjan, 1964
X. dentatum	Sturhan, 1978
X. diversicaudatum *+	(Micoletzky, 1927) Thorne, 1939
X. elongatum	Schuurmans Stekhoven and Teunissen, 1938
X. ensiculiferum	(Cobb, 1893) Thorne, 1937
X. globosum	Sturhan, 1978
X. index *+	Thorne and Allen, 1950
X. ingens	Luc and Dalmasso, 1963
X. insigne	Loos, 1949
X. israeliae	Luc, Brown and Cohn, 1982
X. italiae *+	Meyl, 1953
X. neovuittenezi	Dalmasso, 1969
X. pachtaicum	(Tulaganov, 1938) Kiryanova, 1951
X. pini	Heyns, 1965
X. pyrenaicum	Dalmasso, 1969
X. rivesi *	Dalmasso, 1969
X. rotundatum	Schuurmans Stekhoven and Teunissen, 1938
X. sahelense	Dalmasso, 1969
X. turcicum	Luc and Dalmasso,1963
X. vuittenezi *	Luc, Lima, Weischer and Flegg, 1964

Xiphinema Species Inquirendae

X. grande	Steiner, 1914
X. makrodorum	Vanha, 1893

S. epimikis	(Dalmasso, 1969) Khan et al., 1978
S. maximus *	(Butschli, 1874) Khan et al., 1978
S. remeyi	(Altherr, 1963) Khan et al., 1978

P. georgiensis	(Tulaganov, 1937) Khan et al., 1978

* species reported transmitting virus
\+ species accepted as virus vectors by Trudgill et al. (1983)

TABLE 3 : European Longidoroidea and the countries in which they have been recorded.

Longidorus africanus
Egypt
Greece
Israel
Jordan

Longidorus apulus
Italy
Yugoslavia

Longidorus attenuatus
Belgium
Bulgaria
England
France
Netherlands
Poland
Spain
West Germany

Longidorus caespiticola
Belgium
Channel Islands
Eire
England
France
Netherlands
Scotland
Spain
Wales
West Germany

Longidorus closelongatus
Bulgaria
France

Longidorus cohni
Israel

Longidorus congoensis
Algeria

Longidorus cylindricaudatus
Belgium
Netherlands
West Germany

Longidorus elongatus
Belgium
Bulgaria
Channel Islands
Denmark
East Germany

Longidorus elongatus (cont'd)
Eire
England
Finland
France
Greece
Hungary
Italy
Netherlands
Northern Ireland
Norway
Poland
Scotland
Spain
Sweden
Wales
West Germany

Longidorus euonymus
Bulgaria
Czechoslovakia

Longidorus fasciatus
Greece
Italy

Longidorus globulicauda
France

Longidorus goodeyi
Belgium
Bulgaria
Channel Islands
Eire
England
France
Netherlands
Northern Ireland
Scotland
West Germany

Longidorus intermedius
Belgium
Netherlands
West Germany

Longidorus juvenilis
France
Italy

TABLE 3 : continued

Longidorus laevicapitatus
Egypt
France
Israel
Jordan

Longidorus leptocephalus
Belgium
Denmark
Eire
England
Netherlands
Northern Ireland
Norway
Scotland
Sweden
Wales
West Germany

Longidorus macrosoma
Austria
Belgium
Czechoslovakia
East Germany
Eire
England
France
Italy
Netherlands
Spain
Wales
West Germany
Yugoslavia

Longidorus macroteromucronatus
East Germany

Longidorus paraelongatus
East Germany
West Germany

Longidorus pisi
Bulgaria
Cyprus
Egypt
Israel
Jordan

Longidorus poessneckensis
East Germany

Longidorus profundorum
Belgium
Bulgaria
East Germany
England
France
Netherlands
Northern Ireland
Spain
Wales
West Germany

Longidorus protae
Italy

Longidorus psuedoelngatus
West Germany

Longidorus sylphus
Bulgaria

Longidorus taniwha
Egypt
France
Israel

Longidorus tarjani
France

Longidorus vineacola
Belgium
Bulgaria
Eire
England
France
Israel
Jordan
Netherlands
West Germany

Paralongidorus georgiensis
Egypt

Siddiqia epimikis
Algeria

TABLE 3 : continued

Siddiqia maximus
Algeria
Austria
Czechoslovakia
England
France
Greece
Hungary
Poland
Portugal
Scotland
West Germany

Siddiqia remeyi
France

Xiphinema algeriense
Algeria

Xiphinema americanum
Yugoslavia

Xiphinema basilgoodeyi
Yugoslavia

Xiphinema brevicolle
Austria
Bulgaria
Czechoslovakia
East Germany
France
Hungary
Israel
Italy
Poland
Portugal
Romania
Spain
Switzerland
West Germany

Xiphinema clavatum
Italy

Xiphinema coxi
Belgium
East Germany
England
France
Netherlands
Poland
Spain
West Germany

Xiphinema dentatum
West Germany

Xiphinema diversicaudatum
Belgium
Bulgaria
Channel Islands
Czechoslovakia
Denmark
East Germany
Eire
England
France
Greece
Hungary
Italy
Netherlands
Northern Ireland
Norway
Poland
Portugal
Scotland
Sweden
Switzerland
Wales
West Germany
Yugoslavia

Xiphinema elongatum
Algeria
Egypt
Israel

Xiphinema ensiculiferum
Israel

Xiphinema globosum
West Germany

Xiphinema index
Algeria
Bulgaria
Cyprus
France
Greece
Hungary
Israel
Italy
Jordan
Lebanon
Poland
Portugal
Romania
Spain
Switzerland
Tunisia

TABLE 3 : continued

Xiphinema index (cont'd)
Turkey
West Germany
Yugoslavia

Xiphinema ingens
Cyprus
Israel
Italy
Jordan
Spain
Turkey

Xiphinema insigne
Egypt
Israel
Jordan

Xiphinema israeliae
Israel

Xiphinema italiae
Algeria
Bulgaria
Cyprus
Egypt
France
Greece
Israel
Italy
Portugal
Romania
Spain
Tunisia
Yugoslavia

Xiphinema neovuittenezi
Bulgaria
France
Spain
Yugoslavia

Xiphinema pachtaicum
Algeria
Bulgaria
Cyprus
Egypt
England
France
Greece
Hungary
Israel
Italy
Jordan
Lebanon
Malta

Xiphinema pachtaicum (cont'd)
Morocco
Norway
Poland
Portugal
Romania
Spain
Switzerland
Tunisia
Turkey
West Germany
Yugoslavia

Xiphinema pini
Yugoslavia

Xiphinema pyrenaicum
France
Spain

Xiphinema rivesi
France
Spain
West Germany

Xiphinema rotundatum
Hungary
Yugoslavia

Xiphinema sahalense
Algeria
Portugal
Spain

Xiphinema turcicum
Algeria
Bulgaria
Israel
Italy
Spain
Turkey

Xiphinema vuittenezi
Austria
Bulgaria
Channel Islands
Czechoslovakia
England
France
Hungary
Italy
Jordan
Poland
Portugal
Romania
Spain

TABLE 3 : continued

Xiphinema vuittenezi (cont'd)
Switzerland
West Germany
Yugoslavia

TABLE 4 : Longidoroidea present in European countries.

ALGERIA
Longidorus congoensis
Siddiqia epimikis
maximus
Xiphinema algeriense
elongatum
index
italiae
sahelense
pachtaicum
turcicum

AUSTRIA
Siddiqia maximus
Xiphinema brevicolle
vuittenezi

BELGIUM
Longidorus attenuatus
caespiticola
cylindricaudatus
elongatus
goodeyi
intermedius
leptocephalus
macrosoma
profundorum
vineacola
Xiphinema coxi
diversicaudatum

BULGARIA
Longidorus attenuatus
closelongatus
elongatus
goodeyi
euonymus
pisi
profundorum
sylphus
vineacola
Xiphinema brevicolle
diversicaudatum
index
italiae
neovuittenezi
pachtaicum
turcicum
vuittenezi

CHANNEL ISLANDS
Longidorus caespiticola
elongatus
Xiphinema diversicaudatum
vuittenezi

CYPRUS
Longidorus pisi
Xiphinema index
ingens
italiae
pachtaicum

CZECHOSLOVAKIA
Longidorus euonymus
macrosoma
Siddiqia maximus
Xiphinema brevicolle
diversicaudatum
vuittenezi

DENMARK
Longidorus elongatus
leptocephalus
Xiphinema diversicaudatum

EAST GERMANY
Longidorus elongatus
macrosoma
macroteromucronatus
paraelongatus
poessneckensis
profundorum
Xiphinema brevicolle
coxi
diversicaudatum

EGYPT
Longidorus africanus
laevicapitatus
pisi
taniwha
Siddiqia georgiensis
Xiphinema elongatum
insigne
italiae
pachtaicum

Eire
Longidorus caespiticola
elongatus
goodeyi
leptocephalus
macrosoma
vineacola
Xiphinema diversicaudatum

ENGLAND
Longidorus attenuatus
caespiticola

TABLE 4 : continued

ENGLAND (cont'd)
Longidorus elongatus
goodeyi
leptocephalus
macrosoma
profundorum
vineacola
Siddiqia maximus
Xiphinema coxi
diversicaudatum
pachtaicum
vuittenezi

FINLAND
Longidorus elongatus

FRANCE
Longidorus attenuatus
caespiticola
closelongatus
elongatus
globulicauda
goodeyi
juvenilis
laevicapitatus
macrosoma
profundorum
taniwha
tarjani
vineacola
Siddiqia maximus
remeyi
Xiphinema brevicolle
coxi
diversicaudatum
index
italiae
pachtaicum
pyrenaicum
vuittenezi

GREECE
Longidorus africanus
elongatus
fasciatus
Siddiqia maximus
Xiphinema diversicaudatum
index
italiae
pachtaicum

HUNGARY
Longidorus elongatus
Siddiqia maximus
Xiphinema brevicolle
diversicaudatum
index
pachtaicum
rotundatum
vuittenezi

ISRAEL
Longidorus africanus
cohni
laevicapitatus
pisi
taniwha
vineacola
Xiphinema brevicolle
elongatum
ensiculiferum
index
ingens
insigne
israeliae
italiae
pini
pachtaicum
turcicum

ITALY
Longidorus apulus
elongatus
fasciatus
juvenilis
macrosoma
protae
Xiphinema brevicolle
clavatum
diversicaudatum
italiae
pachtaicum
turcicum
vuittenezi

JORDAN
Longidorus africanus
laevicapitatus
pisi
vineacola

TABLE 4 :continued

JORDAN (cont'd)
Xiphinema index
ingens
insigne
pachtaicum
vuittenezi

LEBANON
Xiphinema index
pachtaicum

MALTA
Xiphinema pachtaicum

MOROCCO
Xiphinema pachtaicum

NETHERLANDS
Longidorus attenuatus
caespiticola
cylindricaudatus
goodeyi
intermedius
elongatus
leptocephalus
macrosoma
profundorum
vineacola
Xiphinema coxi
diversicaudatum

NORTHERN IRELAND
Longidorus elongatus
goodeyi
leptocephalus
profundorum
Xiphinema diversicaudatum

NORWAY
Longidorus elongatus
leptocephalus
Xiphinema diversicaudatum
pachtaicum

POLAND
Longidorus attenuatus
caespiticola
elongatus
euonymus
leptocephalus
Siddiqia maximus
Xiphinema brevicolle
diversicaudatum
index
pachtaicum
vuittenezi

PORTUGAL
Siddiqia maximus
Xiphinema brevicolle
diversicaudatum
index
italiae
pachtaicum
sahelense
vuittenezi

ROMANIA
Xiphinema brevicolle
index
italiae
pachtaicum
vuittenezi

SCOTLAND
Longidorus caespiticola
elongatus
goodeyi
leptocephalus
vineacola
Siddiqia maximus
Xiphinema diversicaudatum

SPAIN
Longidorus attenuatus
caespiticola
elongatus
goodeyi
macrosoma
profundorum
Xiphinema brevicolle
coxi
diversicaudatum
index
ingens
italiae
neovuittenezi
pachtaicum
pyrenaicum
rivesi
sahelense
turcicum
vuittenezi

SWEDEN
Longidorus elongatus
leptocephalus
Xiphinema diversicaudatum

SWITZERLAND
Xiphinema brevicolle
diversicaudatum
index
pachtaicum
vuittenezi

TABLE 4 : continued

TUNISIA
Xiphinema index
italiae
pachtaicum

TURKEY
Xiphinema index
ingens
pachtaicum

WALES
Longidorus caespiticola
elongatus
goodeyi
leptocephlus
macrosoma
profundorum
Xiphinema diversicaudatum

WEST GERMANY
Longidorus attenuatus
caespiticola
cylindricaudatum
elongatus
goodeyi
intermedius
leptocephalus
macrosoma
paraelongatus
profundorum
pseudoelongatus
vineacola

WEST GERMANY (cont'd)
Siddiqia maximus
Xiphinema brevicolle
coxi
dentatum
diversicaudatum
globosum
index
rivesi
vuittenezi

YUGOSLAVIA
Longidorus apulus
macrosoma
Xiphinema americanum
basilgoodeyi
diversicaudatum
index
italiae
neovuittenezi
pachtaicum
rotundatum
vuittenezi

No information available or no report of the occurrence of Longidoroidea in the following countries :-

ALBANIA, ANDORRA, BALEARIC ISLANDS, LIBYA, LIECHTENSTEIN,

LUXEMBOURG, MONACO, SAN MARINO and SYRIA.

TABLE 5 : Tentative morphological/anatomical/geographical groups of Longidorus species.

Group A : Species with distinctly expanded lip region offset from neck contour.

Subgroup A1 : amphidial pouch without basal lobes.

AFRICAN/ASIAN	NORTH AMERICAN
L. martini (a,V)	L. diadecturus (V)

Subgroup A2 : amphidial pouch with basal lobes.

AFRICAN/ASIAN 1	EUROPEAN*
L. monile (a)	L. vineacola (a)
	L. apulus (V)
AFRICAN/ASIAN 2	L. attenuatus (V)
L. pisi	L. closelongatus
	L. euonymus (V)
	L. juvenilis
	L. protae
	L. pseudoelongatus

Group B : Species with a cylindrical anterior region with a lip region continuous with, or only slightly offset from, the neck contour.

AFRICAN 1	ASIAN	EUROPEAN	NORTH AMERICAN 1
L. cohni (a)	L. saginus (a)	L. elongatus (a,V)	L. edmundsi (a)
L. africanus	L. longicaudatus	L. cylindricaudatus	
	L. macromucronatus	L. globulicauda	NORTH AMERICAN 2
AFRICAN 2	L. mirus	L. intermedius	L. tarjani (a)
L. monoloides (a)	L. reneyii	L. leptocephalus (V)	L. breviannulatus
		L. paraelongatus	L. crassus
AFRICAN 3		L. tardicauda	L. fragilis
L. heynsi			L. sylphus

Group C : Species with a conoidal anterior region and rounded lip region continuous with the neck contour.

AFRICAN	ASIAN	AUSTRALASIAN	EUROPEAN
L. belondiroides (a)	L. nirulai (a)	L. taniwha (a)	L. caespiticola (a,V)
L. congoensis	L. indicus		
L. laevicapitatus	L. jonesi		
	L. psidi		

Group D : Species with a conoidal anterior region and a truncate lip region continuous with the neck contour.

EUROPEAN 1
L. macrosoma (a,V)
L. fasciatus (V)
L. goodeyi
L. macroteromucronatus

EUROPEAN 2
L. profundorum (a,V)
L. poessneckensis

(a), amphimictic species.
(V), species reported to transmit virus.
*, species are listed alphabetically after the amphimictic ancestral species.

TABLE 6 : Tentative morphological/anatomical/geographical groups of Xiphinema species present in Europe (abridged and adapted from Luc, 1979).

Group A : Species with one female genital branch reduced or absent.

Subgroup Ad : in this subgroup no trace of an anterior genital branch can be recognised.

OCEANIA

X. ensiculiferum

Group B : The so-called "X. americanum group" comprised of 24 species which are very difficult to differentiate from one another.

EUROPEAN	NORTH AMERICAN
X. brevicolle (V)	X. americanum (V)
X. pachtaicum	X. rivesi (V)

Group C : Species with two genital branches equally developed and with a Z differentiation in the uterus.

Subgroup Ca : presence of a true Z organ i.e. a rather well defined structure, muscular (circular muscles), with lumen cuticularized (or very refringent) and a small number (3-5) of "teeth" very refringent, attached to the wall.

AFRICAN	EUROPEAN
X. rotundatum	X. algeriense (a)

Subgroup Cb : presence of a pseudo Z organ, i.e. a less differentiated structure : wall not muscular and not so well differentiated as in Z organ : no "teeth" but granular structures of variable appearance.

AFRICAN	EUROPEAN 1 *
X. pini (a)	X. diversicaudatum (a,V)
	X. coxi (V)
	X. dentatum
	X. globosum
	EUROPEAN 2
	X. ingens (a)
	X. turcicum

Group D : Species with both genital branches of approximately equal development, and without uterine differentiation (to the exclusion of group B or "X. americanum group).

Subgroup Da : tail hemispherical or nearly so without mucro.

AFRICAN

X. clavatum (a)

Subgroup Db : tail hemispherical or of general rounded shape with a peg, bulge or mucro.

AFRICAN	EUROPEAN 1
X. basilgoodeyi	X. israeliae (a)
	X. index (V)

TABLE 6 : continued.

Subgroup Db : continued.

EUROPEAN 2
X. neovuittenezi (a)
X. pyrenaicum
X. vuittenezi (V)

Subgroup Dc : species with a flagellate to long conical tail (c' more than 5).

ASIAN
X. insigne

Subgroup Dd : species with a short conical tail, digitated or not (c' less than 4.5).

AFRICAN	EUROPEAN
X. elongatum	X. sahelense (a)
	X. italiae (V)

(V), species reported to transmit virus.
(a), amphimictic species.
*, species are listed alphabetically after the amphimictic ancestral species.

Figure 1 : Systematic classification of the Longidoroidea.

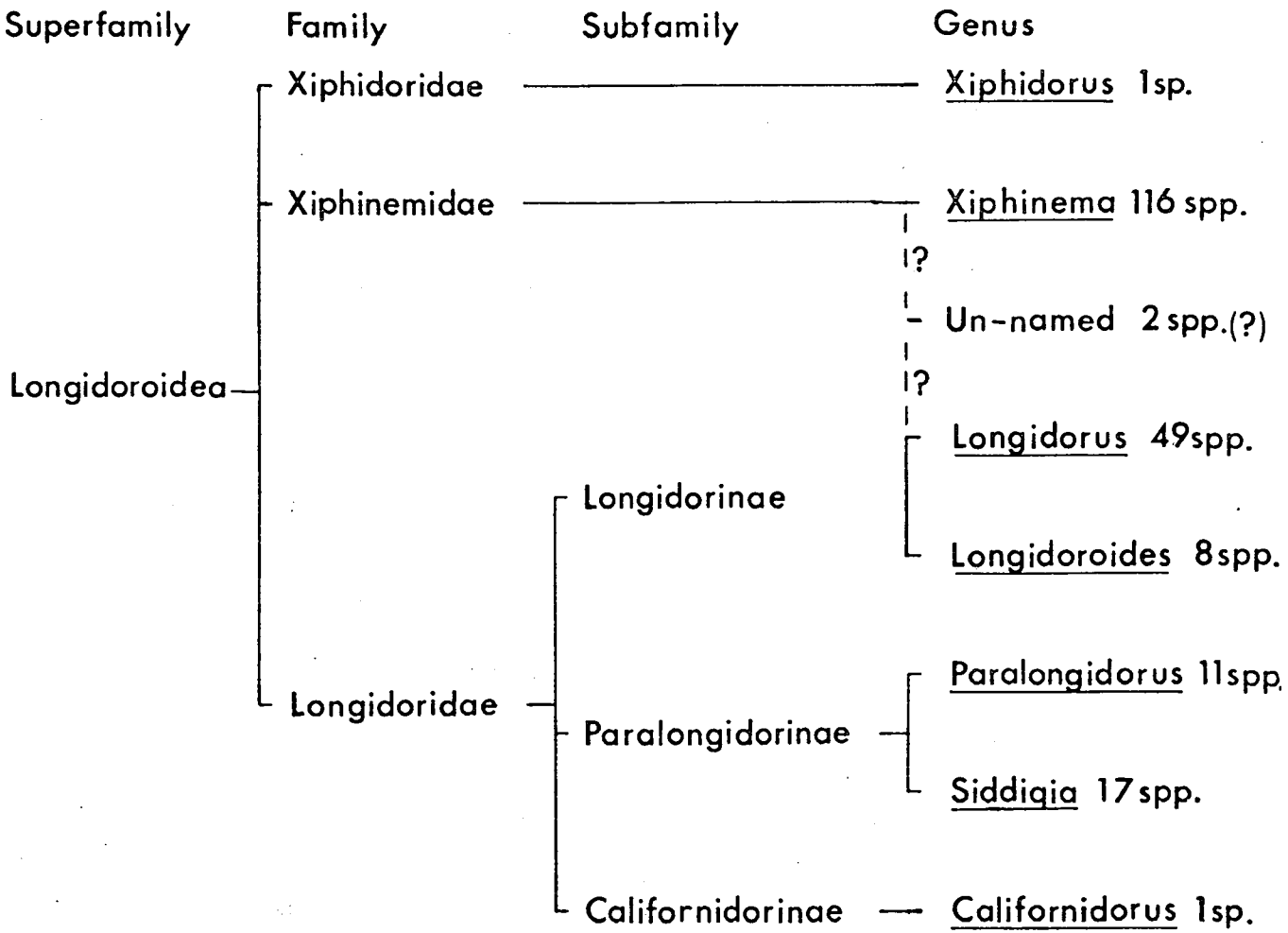


Figure 2: Number of Longidorus, Paralongidorus, Siddiqia and Xiphinema spp., described since 1958.

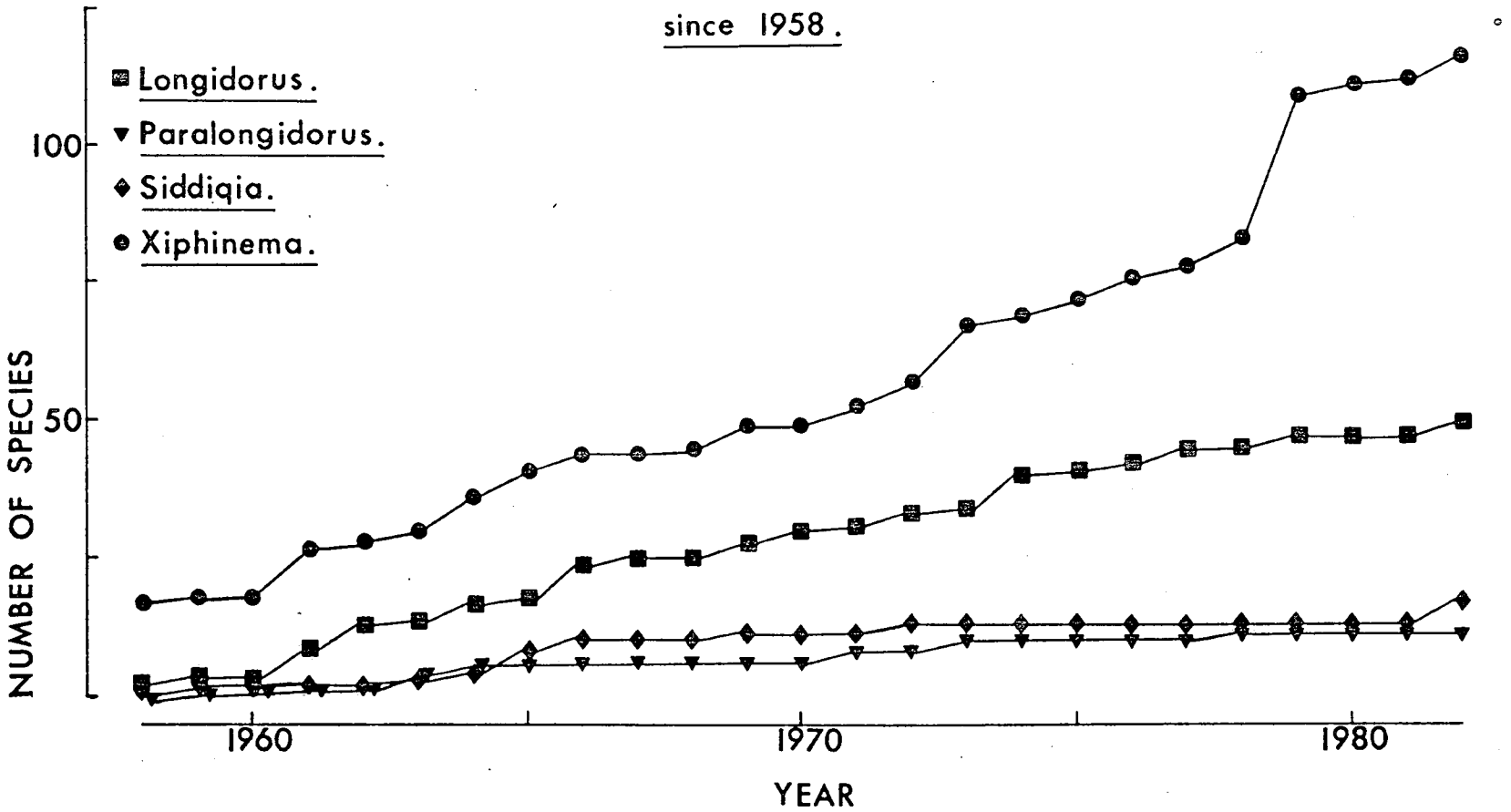


Figure 3 : Number of Longidorus and Xiphinema spp., and virus associations reported since 1958.

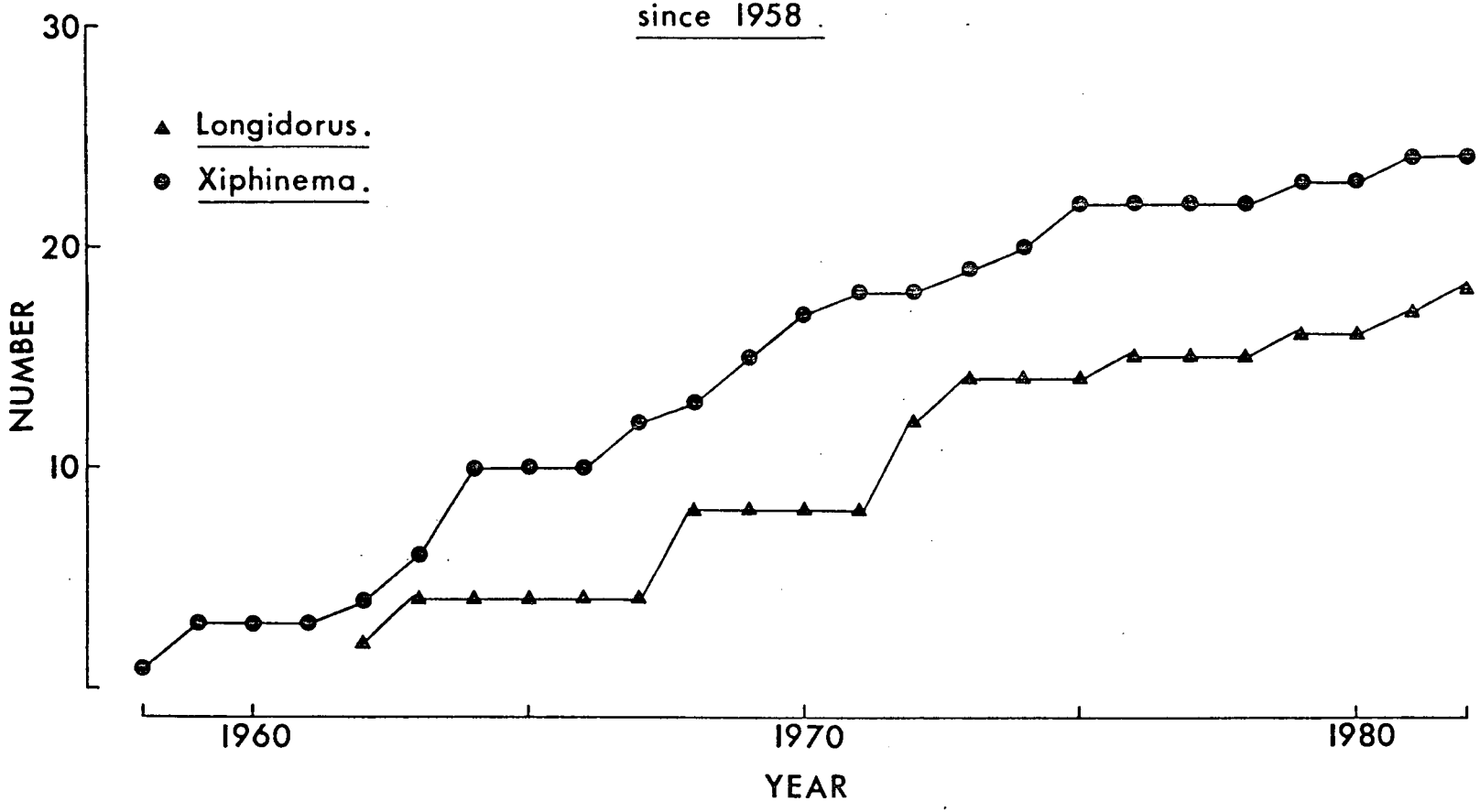


FIGURE 4 : Distribution of Longidorus africanus, ● ; L. apulus, ▲ ; L. attenuatus, O; L. cohni, c; and L. protae, ■ .

Longidorus africanus

Egypt (Aboul-Eid, 1970; Lamberti,1969; Oteifa and Tarjan, 1965; Tarjan, 1964); Greece (Koliopanos and Vovlas, 1977); Israel (Cohn, 1969; Lamberti, 1969); Jordan (Hashim, 1979).

Longidorus apulus

Italy (Lamberti and Bleve-Zacheo, 1977; Rana and Roca, 1973; Roca et al., 1975); Yugoslavia (Lamberti et al., 1973).

Longidorus attenuatus

Belgium (D. De Waele, pers. comm.); Bulgaria (Choleva and Abadzhieva, 1975; Choleva et al., 1980); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Netherlands (J. W. Seinhorst, in litt.); Poland (Brzeski, 1968, 1970; Szczygiel, 1974); Spain (Arias, 1979); West Germany (Forghani et al., 1965; McNamara et al., 1980; Rau, 1975; Rudel, 1974; Weischer, 1966, Wyss, 1969a and b).

Longidorus cohni

Israel (Cohn and Ausher, 1973).

Longidorus protae

Italy (Lamberti and Bleve-Zacheo, 1977; Prota et al., 1971).

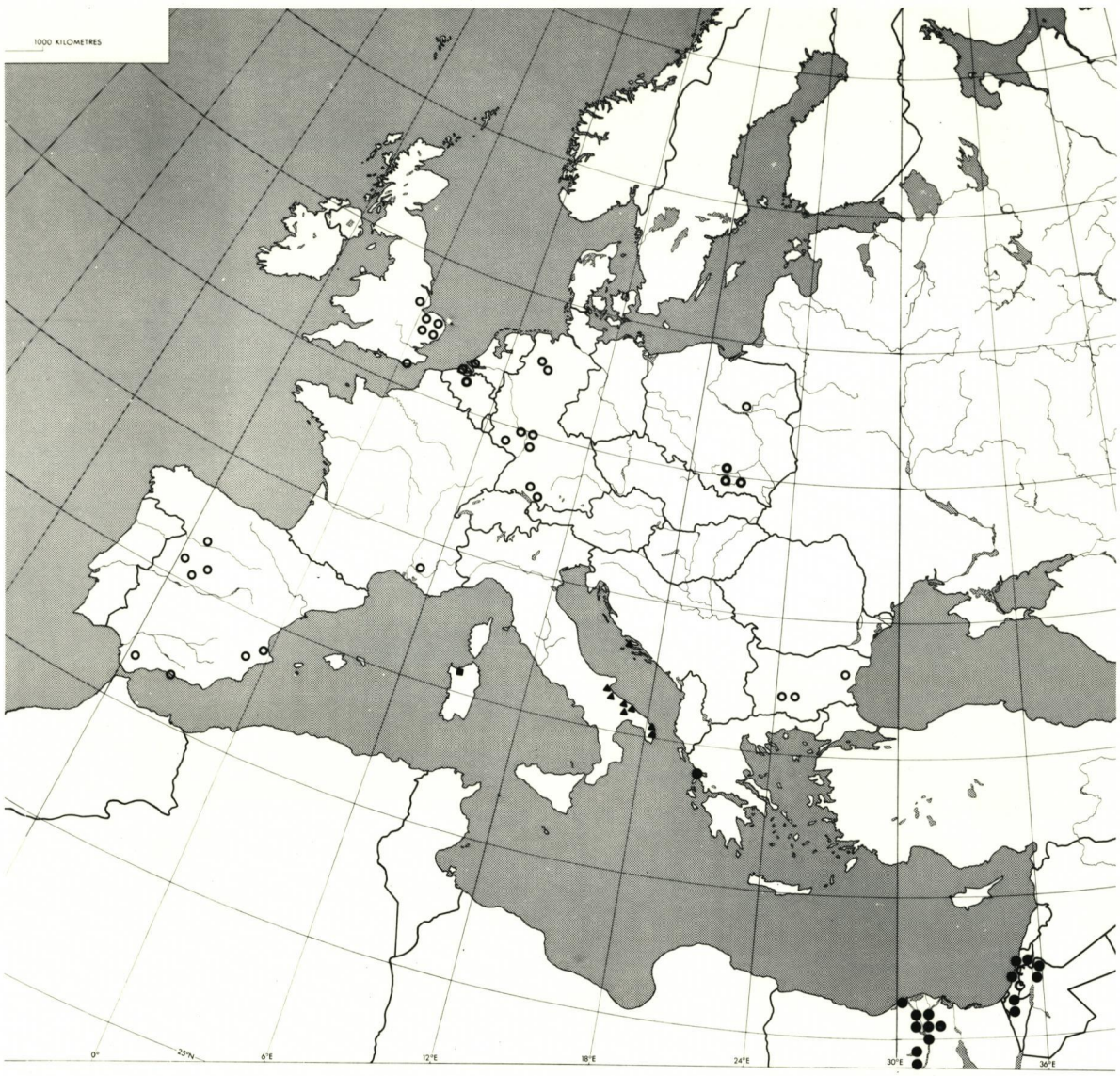

1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 5 : Distribution of Longidorus caespiticola, ● ; L. closelongatus, O; L. cylindricaudatus, ▲ ; L. euonymus, ■ ; and L. fasciatus, f.

Longidorus caespiticola

Belgium (Aboul-Eid, 1970; Coolen and Hendrickx, 1972; D. De Waele, pers. comm.;D'Herde and van den Brande, 1964; Sturhan, 1963); Channel Islands (Brown and Taylor, 1977); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Netherlands (Van Hoof, 1966); Poland (A. Szczygiel, in litt.); Scotland (Brown and Taylor, 1977); Spain (Arias, 1979); Wales (Brown and Taylor, 1977); West Germany (McNamara et al., 1980; Rudel, 1974; Weischer, 1966).

Longidorus closelongatus

Bulgaria (Stoyanov, 1964); France (Dalmasso, 1970, pers. comm.).

Longidorus cylindricaudatus

Belgium (D. De Waele, pers. comm.); Netherlands (Kozlowska and Seinhorst, 1979); West Germany (Kozlowska and Seinhorst, 1979; Rau, 1975).

Longidorus euonymus

Bulgaria (Choleva-Abadzhieva, 1975; Choleva et al., 1980); Czechoslovakia (Mali and Hooper, 1974); Poland (A. Szczygiel, in litt.).

Longidorus fasciatus

Greece (Roca and Lamberti, 1981); Italy (Roca and Lamberti, 1981).

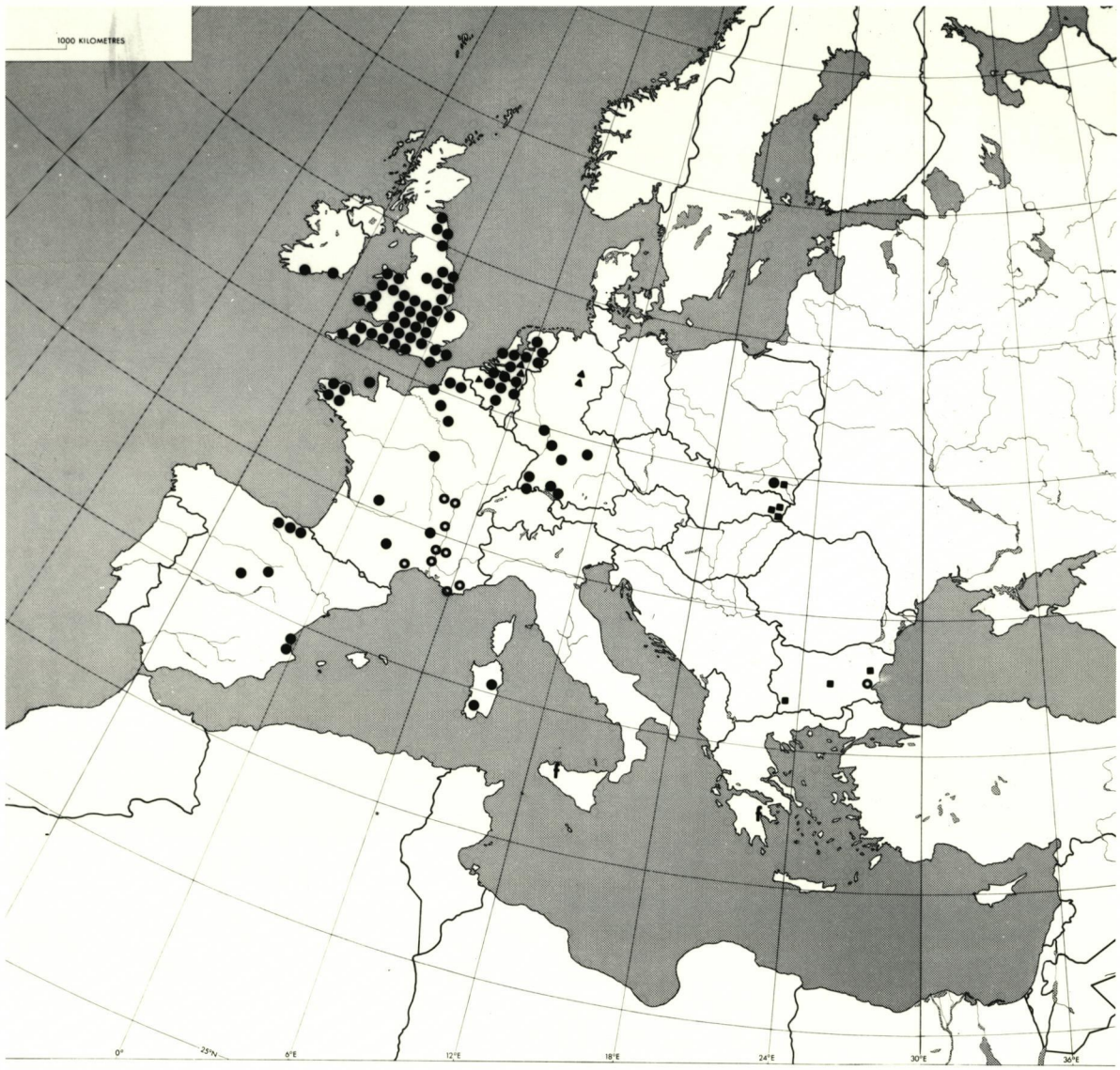

1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 6 : Distribution of Longidorus congoensis C; L. goodeyi ●

L. intermedius, ▲ ; L. juvenilis, O;

L. laevicapitatus, ■ .

Longidorus congoensis

Algeria (Lamberti et al., 1975).

Longidorus goodeyi

Belgium (D. De Waele, pers. comm.); Bulgaria (Stoyanov, 1964); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Netherlands (Van Hoof, 1966); Northern Ireland (Brown and Taylor, 1977); Scotland (Brown and Taylor, 1977); Spain (Arias, 1979); Wales (Brown and Taylor, 1977); West Germany (McNamara et al., 1980; Sturhan, 1963a; Weischer, 1966).

Longidorus intermedius

Belgium (De Waele, pers. comm.);Netherlands (Kozlowska and Seinhorst, 1979); West Germany (Kozlowska and Seinhorst, 1979; Rau, 1975).

Longidorus juvenilis

France (Dalmasso, 1970); Italy (Cotroneo et al., 1980; Lamberti et al., 1980).

Longidorus laevicapitatus

Egypt (Aboul-Eid, 1970; Oteifa and Tarjan, 1965; Tarjan, 1964); France (Dalmasso, 1970); Israel (Cohn, 1969); Jordan (Hashim, 1979).

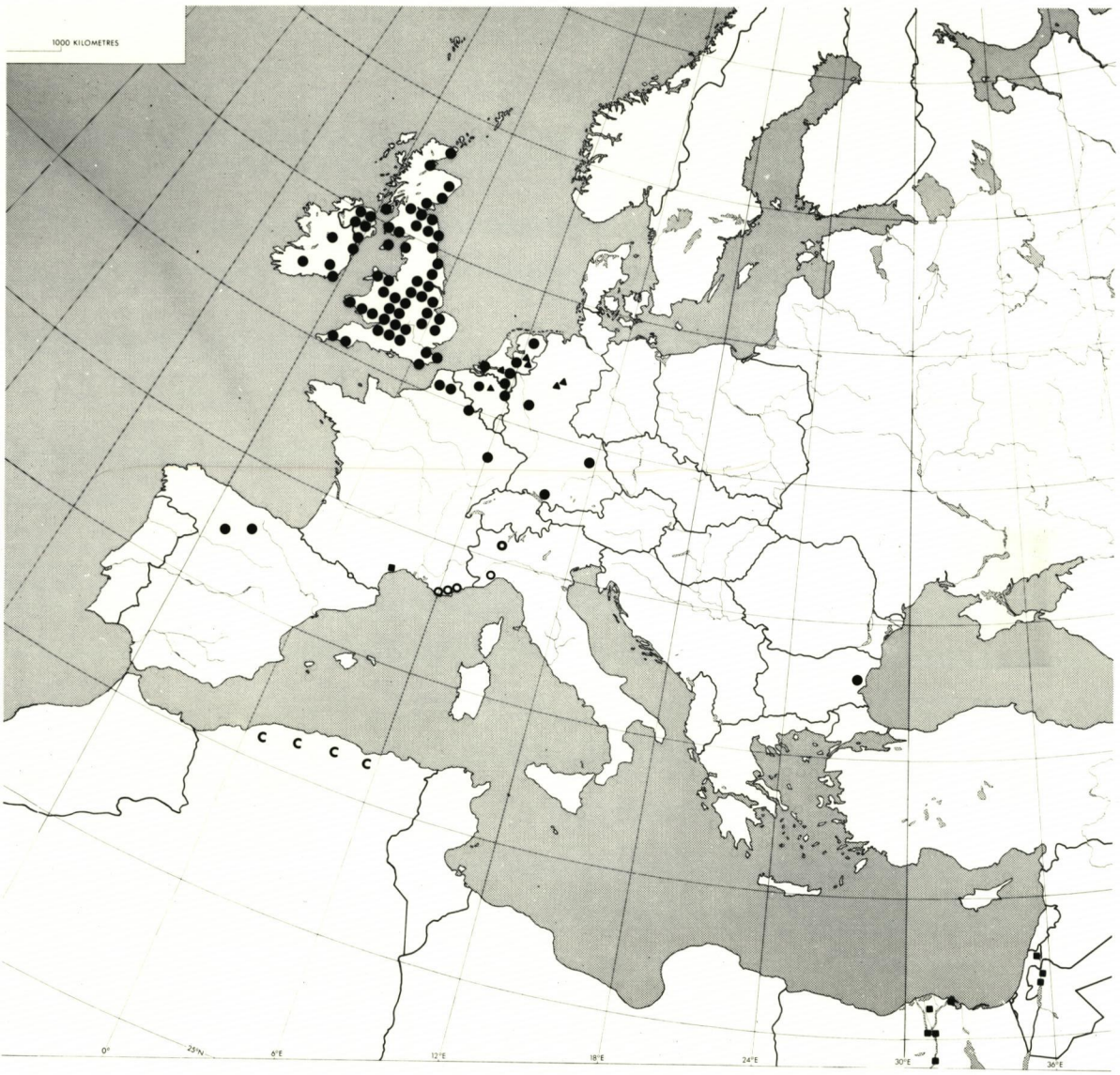

1000 KILOMETRES
0°
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 7 : Distribution of Longidorus elongatus, ● ;

L. macroteromucronatus, O; L. paraelongatus, ▲ ;

L°. poessneckensis, ▣ ; and L. sylphus, S .

Longidorus elongatus Austria (Sturhan, 1963); Belgium (D. De Waele, pers. comm.; D'Herde and van den Brande, 1964); Bulgaria (Choleva-Abadzhieva, 1975); Channel Islands (Brown and Taylor, 1977); Denmark (Jakobson, 1974); East Germany (Fritzsche and Kegler, 1968; Fritzsche et al., 1979); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977); Finland (S. Kurppa, pers. comm.);France (Altherr, 1953; Dalmasso, 1970); Greece (Kyrou, 1964; Terlidou, 1967); Hungary (Andrassy, 1973); Italy (Meyl, 1954); Netherlands (Kozlowska and Seinhorst, 1979; Van Hoof, 1966); Northern Ireland (Brown and Taylor, 1977); Norway (Stoen, 1974); Poland (Brzeski, 1968, 1970; Szczygiel, 1974; Szczygiel et al., 1969; Szczygiel and Hasior, 1972); Scotland (Brown and Taylor, 1977); Spain (Arias, 1979); Sweden (Andersson, 1974; Eriksson,1974); Switzerland (Menzel, 1914); Wales (Brown and Taylor, 1977); West Germany (McNamara et al., 1980; Rau, 1975; Rudel, 1974; Sturhan, 1963a and c; Weischer, 1966; Wyss, 1969a and b).

Longidorus macroteromucronatus

East Germany (Altherr, 1974).

Longidorus paraelongatus

East Germany (Altherr, 1974); West Germany (D. Sturhan pers. comm.).

Longidorus poessneckensis

East Germany (Altherr, 1974)

Longidorus sylphus

Bulgaria (Choleva et al., 1980).

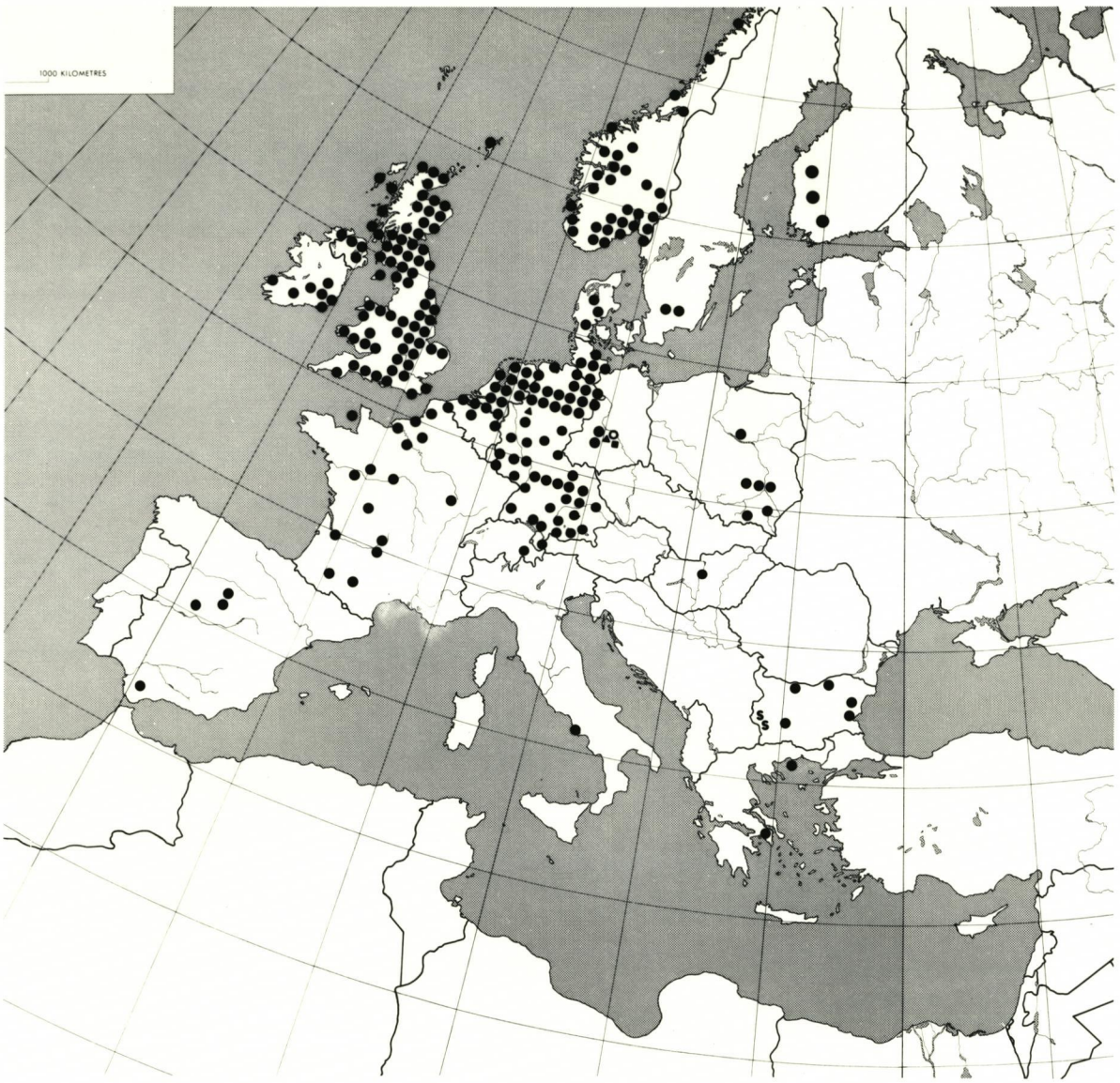

1000 KILOMETRES

FIGURE 8 : Distribution of Longidorus globulicauda, ■ ; L. macrosoma, ● ; L. psuedoelongatus, ▲ ; and L. pisi, O.

Longidorus globulicauda

France (Dalmasso, 1970).

Longidorus macrosoma

Belgium (Coolen and Hendrickx, 1972; D. De Waele, pers. comm.; D'Herde and van den Brande, 1964); Czechoslovakia (Erbenova, 1976); East Germany (Altherr, 1974; Fritzsche, 1968; Fritzsche and Kegler, 1968); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Italy (D'Errico and Ragozzini, 1981; Scognamiglio and Tarjan, 1967); Netherlands (Van Hoof, 1966); Spain (Arias, 1979); Wales (Brown and Taylor, 1977); West Germany (Rau, 1975; Rudel, 1974; Weischer, 1966); Yugoslavia (Lamberti et al., 1976).

Longidorus psuedoelongatus

West Germany (Altherr, 1976).

Longidorus pisi

Bulgaria (Choleva-Abadzhieva, 1975); Cyprus (Philis and Siddiqi, 1976); Egypt (Aboul-Eid, 1972); Israel (Cohn, 1969); Jordan (Hashim, 1979).

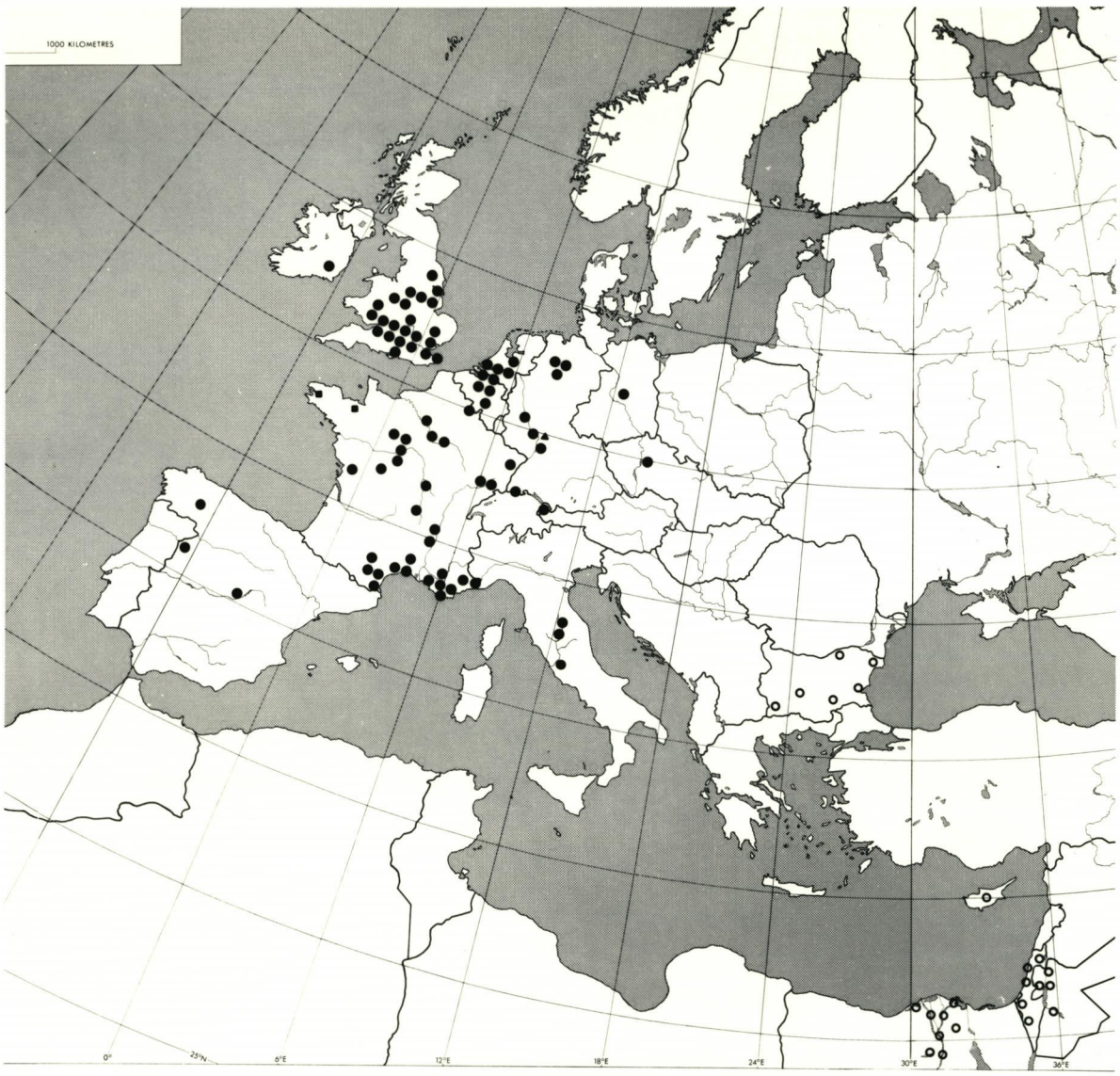

1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 9 : Distribution of Longidorus leptocephalus, ▲ ;

L. profundorum, ● ; L. taniwha, ■ ; L. tarjani, t;

and L. vineacola, O.

Longidorus leptocephalus.

Belgium (D. De Waele, pers. comm.); Denmark (Jakobson, 1974); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977); Netherlands (Van Hoof, 1966); Northern Ireland (Brown and Taylor, 1977); Norway (Stoen, 1975); Scotland (Brown and Taylor, 1977); Poland (A. Szczygiel, pers. comm.); Sweden (Eriksson, 1974); Wales (Brown and Taylor, 1977); West Germany (Rau, 1975; Sturhan, 1963a; Weischer, 1966).

Longidorus profundorum

Belgium (D. De Waele, pers. comm.); Bulgaria (Choleva et al., 1980); East Germany (Fritzsche and Kegler, 1968); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Netherlands (J. W. Seinhorst, pers. comm.); Northern Ireland (Brown and Taylor, 1977); Spain (Arias, 1979); Wales (Brown and Taylor, 1977); West Germany (Rudel, 1974)

Longidorus taniwha

Egypt (Aboul-Eid, 1970; Oteifa and Tarjan, 1965; Tarjan, 1964); France (Dalmasso, 1970); Israel (Cohn, 1969).

Longidorus tarjani

France (Dalmasso, 1970).

Longidorus vineacola

Belgium (Aboul-Eid, 1970; D. De Waele, pers. comm.); Bulgaria (Choleva- Abadzhieva, 1975); Eire (Brown and Taylor, 1977); England (M. Savage, in litt.); France (Dalmasso, 1970); Greece (Terlidou, 1967); Israel (Cohn, 1969); Jordan (Hashim, 1979); Netherlands (J. W. Seinhorst, pers. comm.); West Germany (Rau, 1975; Sturhan and Weischer, 1964; Weischer, 1966; Wyss, 1969a and b).

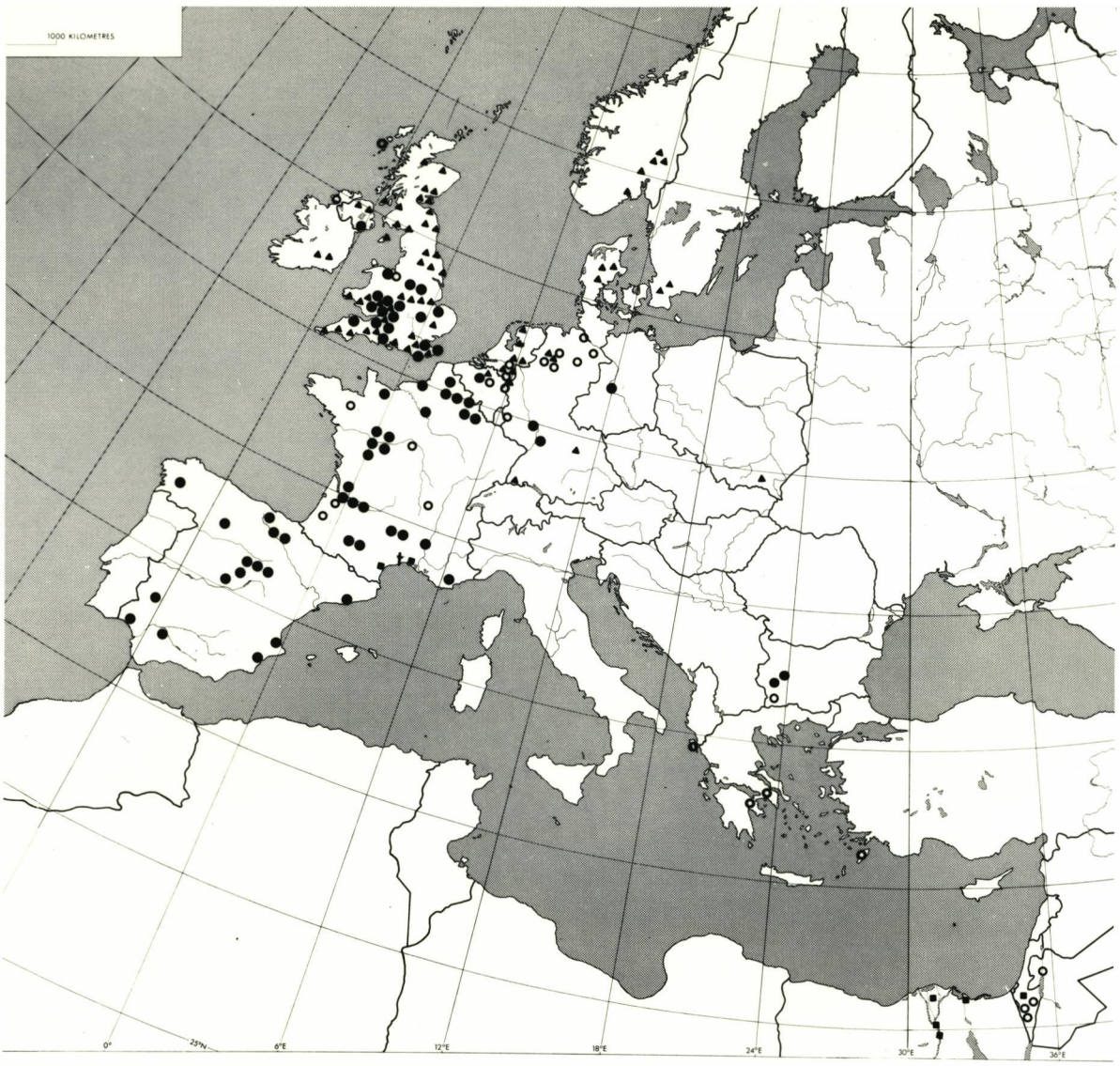

1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 10 : Distribution of Paralongidorus georgiensis, ■ ; S. epimikus, ▲ ; S. maximus, ● ; and S. remeyi, O.

Paralongidorus georgiensis

Egypt (Aboul-Eid, 1970; Oteifa and Tarjan, 1965; Tarjan, 1964).

Siddiqia epimikus

Algeria (Dalmasso, 1970).

Siddiqia maximus

Algeria (Lamberti et al., 1975); Austria (Hoble, 1969); Czechoslovakia (Liskova, 1980; Mali et al., 1975); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Greece (Terlidou, 1967); Hungary (Martelli and Sarospataki, 1969); Poland (Witkowska, 1958); Portugal (Lima, 1966; Macara, 1972); Scotland (Brown and Taylor, 1977; Mabbot, pers. comm.); West Germany (Sprau, 1960; Sturhan, 1963c; Weischer, 1966).

Siddiqia remeyi

France (Altherr, 1963).

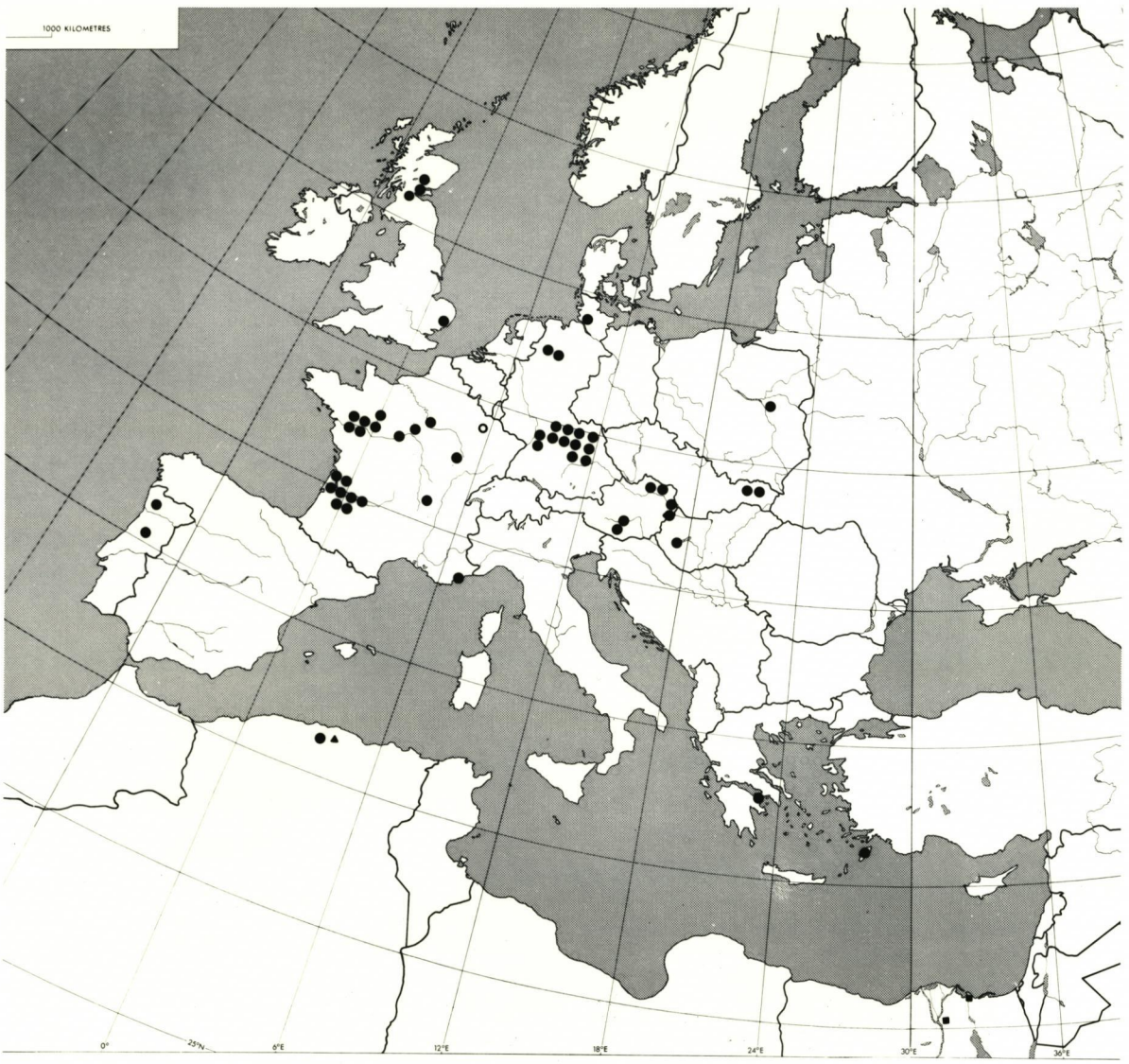

1000 KILOMETRES
0°
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 11 : Distribution of Xiphinema americanum, a;

X. basilgoodeyi, b; X. ensiculiferum, e;

X. italiae, ● ;X. pyrenaicum, ■ ;

X. rotundatum, r; X. neovuittenezi, ▲ ; and

X. vuittenezi, O.

Xiphinema americanum

Yugoslavia (Hrzic, 1978).

Xiphinema basilgoodeyi

Yugoslavia (Hrzic, 1978).

Xiphinema ensiculiferum

Israel (Cohn and Sher, 1972).

Xiphinema italiae

Algeria (Dalmasso and Cuany, 1969); Bulgaria (Choleva-Abadzhieva, 1975; Choleva et al., 1980; Stoyanov, 1964); Cyprus (Antoniou, 1981); Egypt (Oteifa and Tarjan, 1965; Tarjan, 1964); France (Dalmasso, 1970; Martelli et al., 1966); Greece (Terlidou, 1967); Israel (Cohn, 1969; Martelli et al., 1966); Italy (Amici, 1965 and 1967; Martelli et al., 1966; Martelli and Lamberti, 1967; Meyl, 1953; Prota, et al., 1971; Roca and Lamberti, 1978); Portugal (Lima, 1974); Romania (Manolache et al., 1971; Manolache and Romascu, 1973; Romascu, 1971; Zinka et al., 1979); Spain (Arias, 1979); Tunisia (Martelli et al., 1966; Siddiqi, 1964); Yugoslavia (Lamberti et al., 1976).

Xiphinema pyrenaicum

France (Dalmasso, 1970); Spain (Arias, 1979).

Xiphinema rotundatum

Hungary (Andrassy, 1973); Yugoslavia (Hrzic, 1978).

Xiphinema neovuittenezi

Bulgaria (Choleva-Abadzhieva, 1975); France (Dalmaso, 1970); Spain (Arias, 1979); Yugoslavia (Hrzic, 1978).

Xiphinema vuittenezi

Austria (Hobl, 1969); Bulgaria (Choleva-Abadzhieva, 1975; Choleva, et al., 1980);Channel Islands (Brown and Taylor, 1977); Czechoslovakia (Erbenova, 1975; Liskova, 1980; Mali and Hooper, 1974; Mali and Vanek, 1973; Mali et al., 1975); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Hungary (Mali et al., 1975; Martelli and Sarospataki, 1969); Italy (Amici, 1965 and 1967; Lamberti et al., 1980; Martelli and Lamberti, 1967; Roca and Lamberti, 1978); Jordan (Hashim, 1979; Szczygiel, 1974; Szczygiel and Hasior, 1972); Portugal (Luc et al., 1964); Poland (Brzeski, 1970); Romania (Romascu and Zinka, 1977; Zinca et al., 1979); Spain (Arias, 1979); Switzerland

(Anon, 1966 and 1974); West Germany (Luc et al., 1964; Rau, 1975; Rudel, 1971 and 1974; Weischer, 1966); Yugoslavia (Hrzic, 1978).

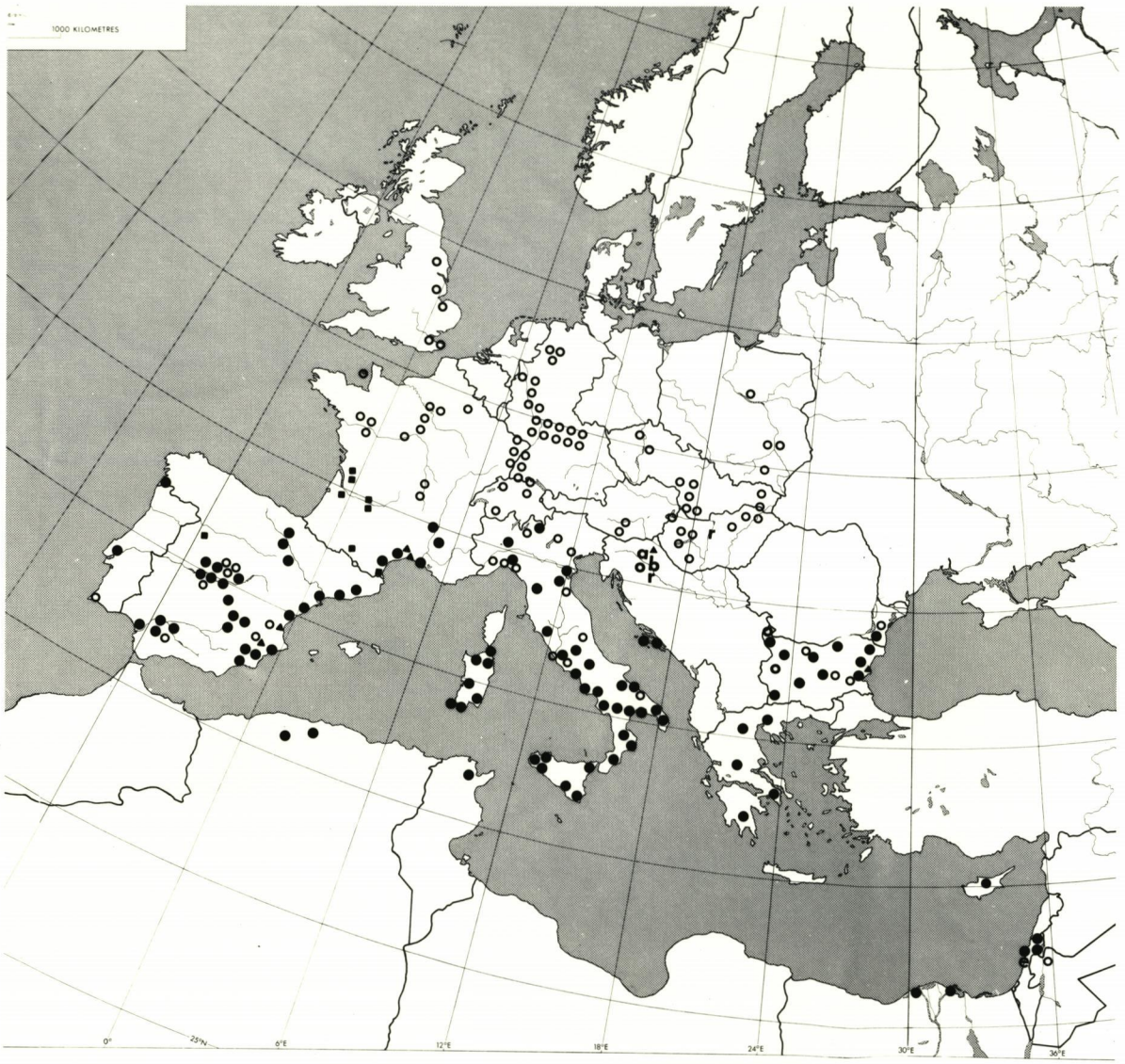

1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 12 : Distribution of Xiphinema algeriense, a;

X. brevicolle, O; X. clavatum, c; X. coxi, ▲ ;

X. dentatum, ■ ; X. diversicaudatum, ● ; and

X. israeliae, i.

Xiphinema algeriense

Algeria (Luc and Kostadinov, 1981).

Xiphinema brevicolle

Austria (Hoble, 1969); Bulgaria (Choleva-Abadzhieva, 1975); Czechoslovakia (Erbenova, 1975 and 1976; Lamberti and Bleve-Zacheo, 1979; Liskova and Sabova, 1973);East Germany (Fritzsche and Kegler, 1968); France (Dalmasso, 1970); Hungary (Andrassy, 1979; Lamberti and Bleve-Zacheo, 1979);Israel (Cohn, 1969); Italy (Lamberti et al, 1980; Martelli and Lamberti, 1967; Roca and Lamberti, 1978); Poland (Lamberti and Bleve-Zacheo, 1979;Szczygiel, 1974); Portugal (Weischer, 1974); Romania (Zinca et al., 1979); Spain (Arias, 1979); Switzerland (Anon, 1974); West Germany (Weischer, 1974).

Xiphinema clavatum

Italy (Roca and Lamberti, 1978).

Xiphinema coxi

Belgium (D. De Waele, pers. comm.); East Germany (Fritzsche and Kegler, 1968); England (Brown and Taylor, 1977); France (Dalmasso, 1970); Netherlands (Van Hoof, 1971); Poland (Szczygiel, 1974); Spain (Arias, 1979); West Germany (Rau, 1975; Weischer, 1966).

Xiphinema dentatum

West Germany (Sturhan, 1978).

Xiphinema diversicaudatum

Austria (Franz, 1942); Belgium (Coolen and Hendrickx, 1972; D. De Waele, pers. comm.; D'Herde and Brande, 1964); Bulgaria (Choleva, 1970; Choleva et al., 1980); Channel Islands (Brown and Taylor, 1977); Czechoslovakia (Erbenova, 1975 and 1976); Denmark (Jakobson, 1974); East Germany (Fritzsche, 1964 and 1966; Fritzsche and Kegler, 1968; Paesler, 1956); Eire (Brown and Taylor, 1977); England (Brown and Taylor, 1977);France (Dalmasso, 1970); Greece (Terlidou, 1967); Hungary (Andrassy, 1973); Italy (Amici, 1967; Corte, 1968; D'Errico and Ragozzini, 1981; Lamberti et al., 1980; Martelli and Lamberti, 1967; Prota et al., 1971; Raski and Amici, 1964; Roca and Lamberti, 1978); Netherlands (Seinhorst, 1963; Van Hoof, 1966 and 1971); Northern Ireland (Brown and Taylor, 1977); Norway (Stoen, 1975); Poland (Brzeski, 1968 and 1970; Szczygiel, 1974; Szczygiel et al., 1969); Portugal (Macara, 1963); Scotland (Brown and Taylor, 1977); Spain (Arias, 1979); Sweden (Eriksson, 1974); Switzerland (Anon, 1966; Klingler and Kunz, 1978); Wales (Brown and Taylor, 1977); West Germany (Altherr, 1958; Rau, 1975; Rudel, 1971; Sturhan, 1963b and c; Weischer, 1966; Wyss, 1969a and b); Yugoslavia (Hrzic, 1978; Lamberti et al., 1973; Lamberti et al., 1976).

Xiphinema israeliae

Israel (Luc, Brown and Cohn, 1982).

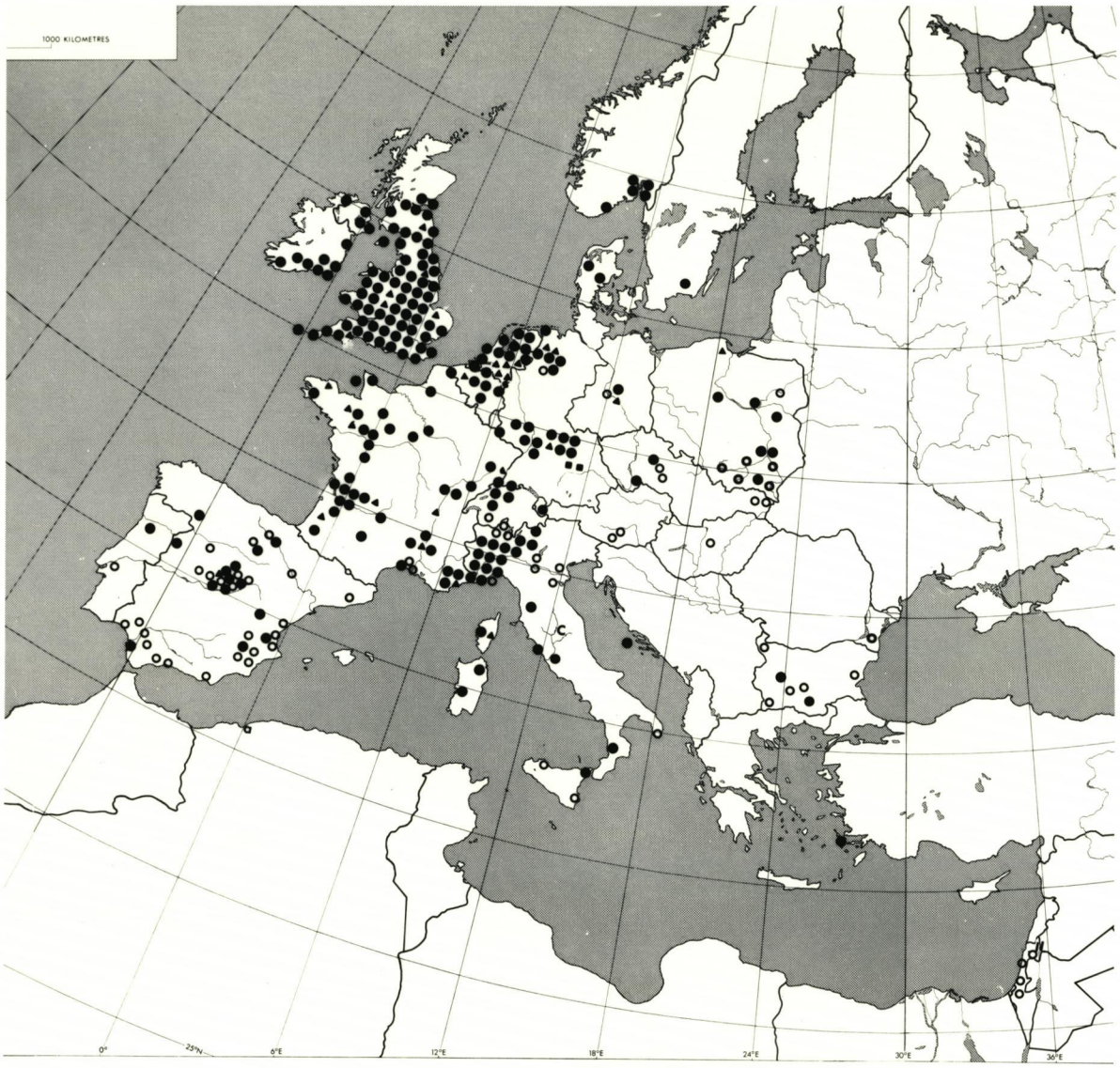

1000 KILOMETRES
0°
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 13 : Distribution of X. elongatum, O; X. globosum, ■ ; X. index, ● ; X. ingens, ▲ .

Xiphinema elongatum

Algeria (Lamberti et al., 1975); Egypt (Oteifa and Tarjan, 1965; Tarjan, 1964); Israel (Cohn, 1969).

Xiphinema globosum

West Germany (Sturhan, 1978).

Xiphinema index

Algeria (Dalmasso and Cuany, 1969; Lamberti et al., 1975); Bulgaria (Choleva-Abadzhieva, 1975); Cyprus (Antoniou, 1981; Philis and Siddiqi, 1976); France (Dalmasso, 1970); Greece (Hirschmann et al., 1966; Koliopanos and Vovlas, 1977; Kyrou, 1964; Terlidou, 1967); Hungary (Mali, 1976; Mali et al., 1975; Martelli and Sarospataki, 1969); Israel (Cohn, 1969); Italy (Amici, 1965 and 1967; Amici et al., 1964; Martelli and Lamberti, 1967; Martelli and Raski, 1963; Prota et al., 1971;Raski and Amici, 1964; Roca and Lamberti, 1978; Scognamiglio and Tarjan, 1967); Jordan (Hashim, 1979); Lebanon (Jalloul, 1971; Taylor et al., 1972); Poland (Glaser and Skowronski, 1970); Portugal (Macara, 1963); Romania (Romascu and Zinka, 1974; Zinka et al., 1979); Spain (Arias, 1979); Switzerland (Anon, 1966 and 1974); Tunisia (Ritter, 1959); Turkey (Tekinal et al., 1972); West Germany (Rudel, 1971 and 1974; Weischer, 1966); Yugoslavia (Hrzic, 1978; Lamberti et al., 1973; Lamberti et al., 1976).

Xiphinema ingens

Cyprus (Antoniou, 1981); Israel (Cohn, 1969); Italy (Martelli and Lamberti, 1967; Roca and Lamberti, 1978); Jordan (Hashim, 1979); Spain (Arias, 1979); Turkey (Luc and Dalmasso, 1963).

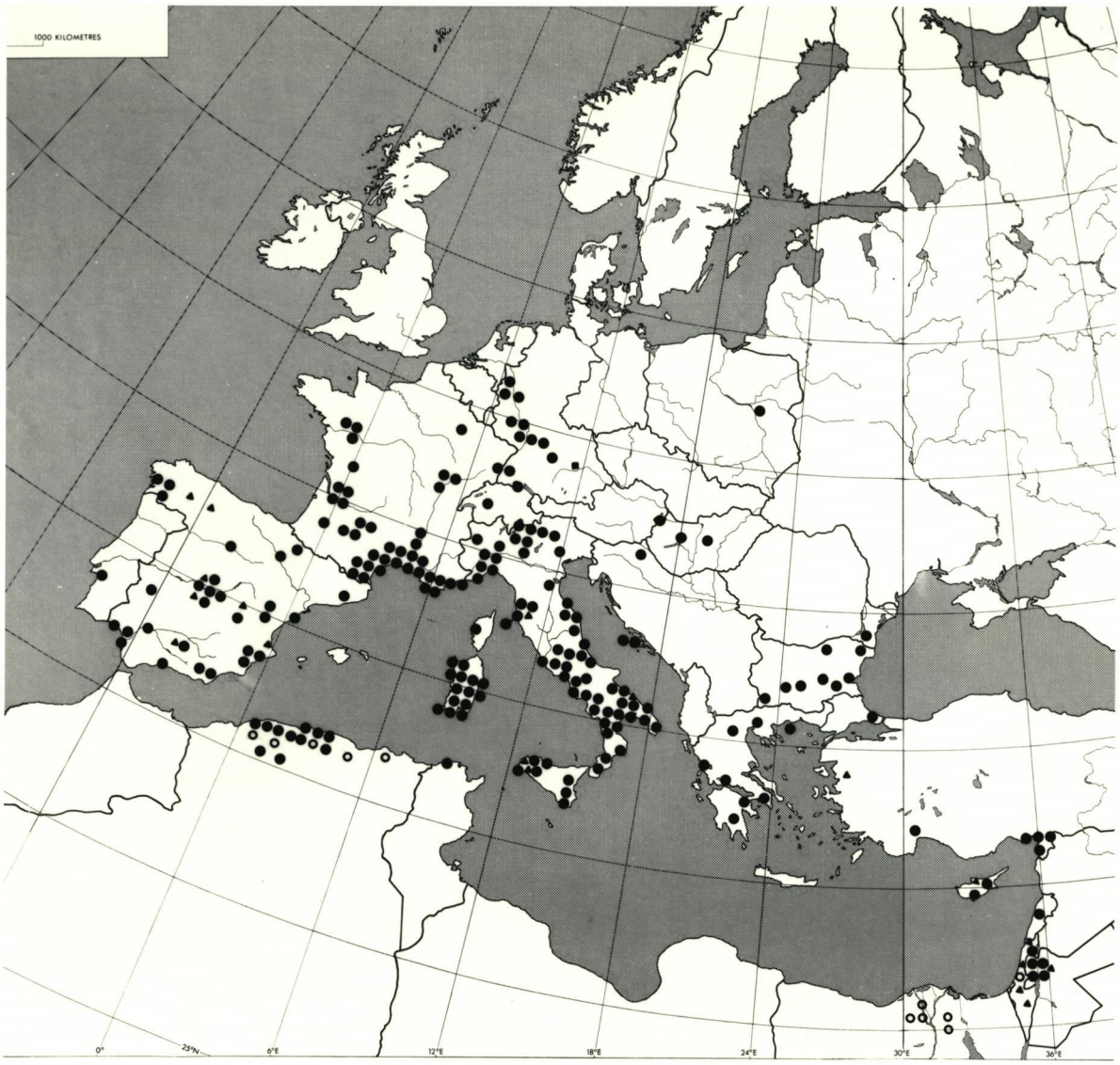

1000 KILOMETRES
0°
25°W
6°E
12°E
18°E
24°E
30°E
36°E

FIGURE 14 : Distribution of Xiphinema insigne, i; X. pachtaicum, ● ; X. pini, p; X. rivesi, ■ ; X. sahelense, ▲ ; X. turcicum, O.

Xiphinema insigne

Egypt (Oteifa and Tarjan, 1965; Tarjan, 1964); Israel (Cohn, 1969); Jordan (Hashim, 1979).

Xiphinema pachtaicum

Algeria (Dalmasso and Cuany, 1969; Lamberti et al., 1975); Bulgaria (Choleva-Abadzhieva, 1975; Choleva et al., 1980; Lamberti and Bleve-Zacheo, 1979; Martelli and Lamberti, 1967; Stoyanov, 1964); Cyprus (Antoniou, 1981; Philis and Siddiqi, 1976); Egypt (Oteifa and Tarjan, 1965; Tarjan, 1964 and 1969); England (Brown and Taylor, 1977); France (Dalmasso, 1970; Lamberti and Bleve-Zacheo, 1979; Martelli and Lamberti, 1967); Greece (Hirschmann et al., 1966; Koliopanas and Vovlas, 1977; Kyrou, 1964; Lamberti and Bleve-Zacheo, 1979; Tarjan, 1969; Terlidou, 1967); Hungary (Lamberti and Bleve-Zacheo, 1979); Israel (Cohn, 1969; Lamberti and Bleve-Zacheo, 1979; Martelli and Lamberti, 1967; Tarjan, 1969); Italy (Amici, 1965 and 1967; Lamberti et al., 1980; Lamberti and Bleve-Zacheo,1979; Lamberti and Martelli, 1967 and 1971; Prota et al., 1971; Raski and Amici,1964; Scognamiglio and Tarjan, 1967; Tarjan, 1969); Jordan (Hashim, 1979); Lebanon (Jalloul, 1971; Taylor et al., 1972); Malta (Lamberti and Siddiqi, 1977); Morocco (Lamberti and Bleve-Zacheo, 1979); Norway (Stoen, pers. comm.); Poland (Wasilewska, 1971); Portugal (Lamberti and Bleve-Zacheo, 1979; Macara, 1963; Tarjan, 1969); Romania (Manolache et al., 1974; Manolache and Romascu, 1973; Romascu, 1971; Zinka et al., 1979);Spain (Arias, 1979); Switzerland (Anon, 1974; Lamberti and Bleve-Zacheo, 1979); Tunisia (Ritter, 1959); Turkey (Lamberti and Bleve-Zacheo, 1979; Tarjan, 1969; Tekinal et al., 1972) West Germany (Rudel, 1971 and 1974); Yugoslavia (Hrzic, 1978; Korunic, 1976; Krnjaic and Krnjaic, 1976; Lamberti and Bleve-Zacheo, 1979).

Xiphinema pini

Israel (Cohn, 1969).

Xiphinema rivesi

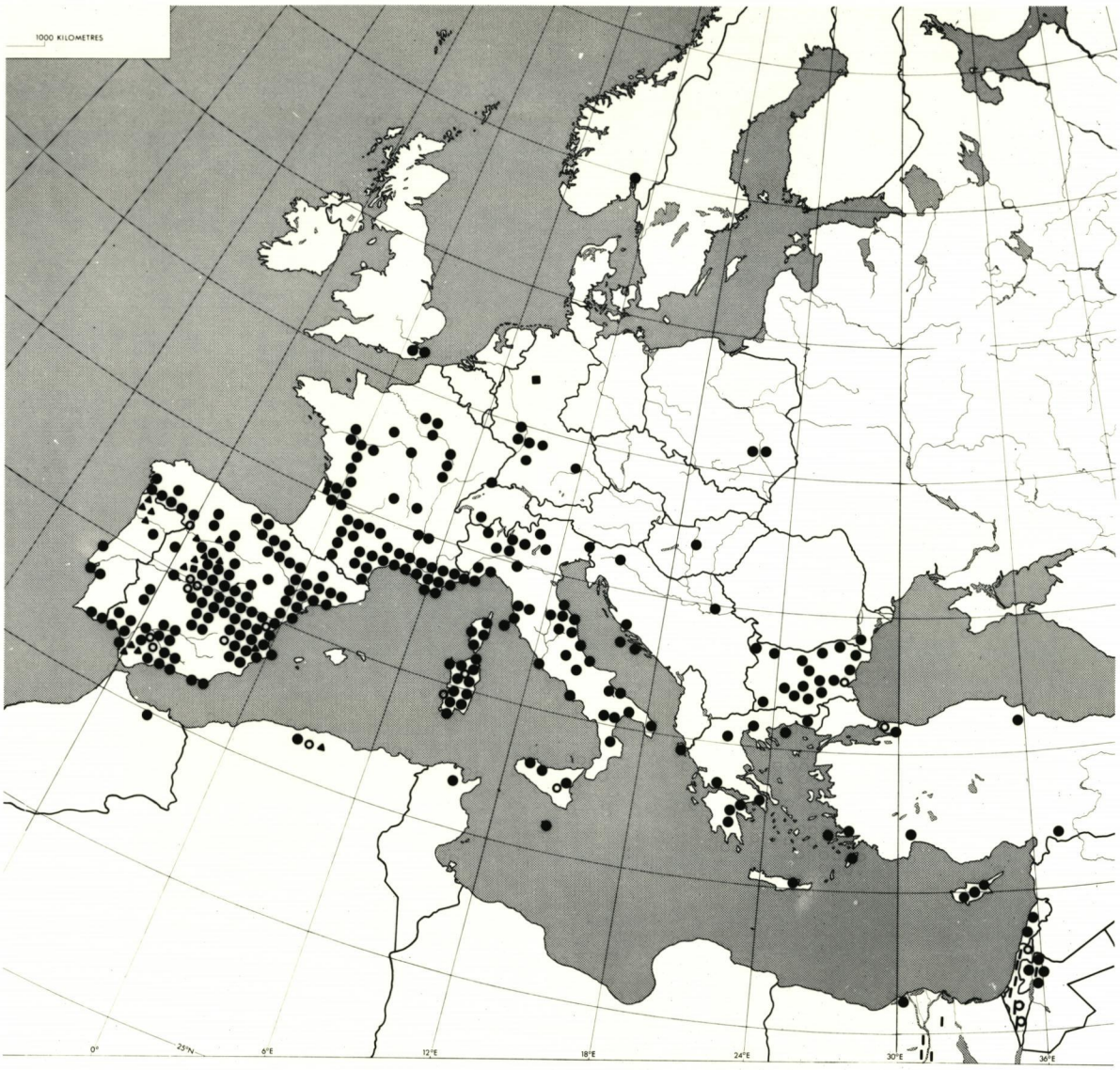
France (Dalmasso, 1970; Lamberti and Bleve-Zacheo, 1979); Spain (Arias and Navacerrada, 1973; Lamberti and Bleve-Zacheo, 1979); West Germany (D. Sturhan, pers. comm.).

Xiphinema sahelense

Algeria (Dalmasso, 1969); Portugal (Macara, 1970 and 1972); Spain (Arias, 1979).

Xiphinema turcicum

Algeria (Dalmasso and Cuany, 1969); Bulgaria (Choleva-Abadzhieva, 1975); Israel (Cohn, 1969); Italy (Prota et al., 1971; Roca and Lamberti, 1978); Spain (Arias, 1979); Turkey (Luc and Dalmasso, 1963).


1000 KILOMETRES
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

CHAPTER III

THE LONGIDOROIDEA OF THE USSR

III : 1 INTRODUCTION AND DATA SOURCES

Many of the research papers reporting Longidoroidea in the USSR do not include details of the exact location of the species recorded. Also, information about the distribution of the species is available for only a few scattered areas and there are few references to host plants. Therefore, only a limited account can be given of the occurrence and distribution of members of the Longidoroidea in the USSR. The following account, based on data contained in c. 50 publications, gives a general indication of their occurrence and distribution in the western half of the USSR.

Kiryanova and Krall (1969) cite 2877 titles of nematological papers published in the USSR up to 1966. In a supplementary list they cited almost 1000 further titles, many of which are papers published in the USSR up to 1970 (Kiryanova and Krall, 1971). Several of the references cited by Kiryanova and Krall (1971) include references to members of the Longidoroidea reported present in the USSR. However, many of the papers cited by these authors are unobtainable and therefore were excluded from the present study. Helminthological Abstracts 1970 to 1981 was used to update the references in Kiryanova and Krall (1971).

III : 2 RESULTS AND DISCUSSION

Seven Longidorus species, two Paralongidorus species and ten Xiphinema species have been reported from the western USSR (Tab. 7). All of them occur in Europe except L. tardicauda, P. nudus and

X. attorodorum. However, the reports of these 19 Longidoroidea refer to only 10 states of the USSR (Tab. 8) so little information is available about the occurrence of Longidoroidea in the western USSR.

L. elongatus is the only longidoroid nematode reported to occur in the two northern USSR states of Estonia and Latvia. Whereas in the central states of Belorussiya, Central (Moscow), Moldavia and the Ukraine six Longidorus species, two Paralongidorus species and nine Xiphinema species have been recorded. In the southern states of Kazakhskaya, Tadzhikskaya, Turkmenskaya and Uzbekskaya only three Longidorus species, two Paralongidorus species and three Xiphinema species have been recorded (Tab. 8).

The earliest records of Longidoroidea in the USSR are probably those of Micoletzky (1923, 1927) who identified L. elongatus, L. caespiticola and X. diversicaudatum from alluvium associated with tributaries of the river Volga. Other early records of Longidoroidea in the USSR are those of Tulaganov (1937, 1938, 1949) who originally described P. georgiensis and X. pachtaicum from the southern USSR, Kiryanova (1951) who originally described P. nudus, also from southern USSR, and Merzkeevskaya (1951, 1953) who originally described L. tardicauda from central USSR.

The distribution of the Longidoroidea in the USSR generally reflects the European distributions of the same species. L. elongatus is the most northerly distributed species in Europe and likewise in the USSR whereas other northern European species such as L. attenuatus and L. caespiticola show similar distribution preferences in the USSR. Southern European species such as L. africanus, X. pachtaicum and X. index similarly show preference for the southern USSR. However, the reports of L. attenuatus and L. caespiticola should perhaps be considered identifications inquirendae due to their locations in the

USSR being considerably outwith their restricted distribution areas in Europe. L. caespiticola was originally identified as L. elongatus by Micoletzky (1927) but subsequently Sturhan (1963a) synonymised these specimens with L. caespiticola. Merzheevskaya (1951) described L. striola from central USSR but Lamberti (1975) subsequently synonymised this species with L. sylphus. X. pachtaicum was originally described by Tulaganov (1938) as L. pachtaicus and subsequently X. mediterraneum (originally described by Martelli and Lamberti, 1967), and was synonymised with X. pachtaicum (Siddiqi and Lamberti, 1977).

It is not known if X. americanum and X. pachtaicum both occur in the USSR because, although both specific names have been used it is possible that the nomenclature refers to only one species, probably X. pachtaicum (Lamberti and Bleve-Zacheo, 1979). However, in the Moscow area tomato ringspot virus, transmitted by X. americanum, was found to be causing damage in raspberry (Waister in litt.) and Koev et al.(1970) reported X. americanum transmitting leaf crinkle virus to black currants. These reports suggest that X. americanum may be present in the USSR because X. pachtaicum has not been reported as a vector of these viruses. However, little is known about the virus vectoring capabilities of X. pachtaicum and thus some uncertainty must remain about the true status of the X. americanum reported from the USSR.

As in Europe, the taxonomy of the Longidoroidea present in the USSR still has to be more clearly defined. Also, the number of species in the USSR will probably increase, as in Europe, as the taxonomy of the Longidoroidea develops and as further research into the occurrence of Longidoroidea continues. Ivanova and Kankina (1972) record the presence of two unidentified Longidorus species in

Tadzhikskaya, and Kiryanova and Shagalina (1969) record the presence of a Xiphinema species, which resembles X. yapoense, associated with grapevine in Kazakhaskaya.

The distribution of Longidoroidea in the USSR probably reflects, even more so than in Europe, the distribution of nematologists who have become interested in this particular superfamily. However, as in Europe, the association of the Longidoroidea with cultivated crops in the USSR probably offers further evidence of the involvement of man in the dissemination of these nematodes.

TABLE 7 : Longidoroidea reported from the U.S.S.R.

Longidorus	africanus
	attenuatus
	caespiticola
	elongatus
	sylphus
	tardicauda
	vineacola
Paralongidorus	georgiensis
	nudus
Xiphinema	americanum
	attorodorum
	brevicolle
	diversicaudatum
	index
	italiae
	opisthohysterum
	pachtaicum
	turcicum
	vuittenezi

TABLE 8 : Longidoroidea reported from different states of the U.S.S.R.

BELORUSSIYA	
Longidorus sylphus	(Merzheevskaya, 1951, 1953; Lamberti, 1975)
caespiticola	(Merzheevskaya, 1951, 1953)
CENTRAL (MOSCOW) U.S.S.R.	
Longidorus attenuatus	(Metlitskii, In: Kiryanova and Krall, 1971; Romanenko, 1971)
caespiticola	(Micoletzky, 1927; Sturhan, 1963)
elongatus	(Kiryanova, 1959; Romanenko, 1971; Teploukhova, 1974)
Xiphinema americanum	(Borzykh, 1972; German, 1968; Romanenko, 1971)
attorodorum	(Romanenko, 1976 In: Stegaresku, 1980)
brevicolle	(Metlitskii, In: Kiryanova and Krall 1971; Romanenko,1970, 1971)
diversicaudatum	(Micoletzky, 1923, 1927; Teploukhova, 1974)
opisthohysterum	(Teploukhova, 1974)
ESTONIA	
Longidorus elongatus	(Krall, 1959, 1964, 1965)
KAZAKHSKAYA	
Longidorus elongatus	(Semkina, 1971a,b)
Xiphinema americanum	(Razzhivin, 1969; Sofrygina, 1974)
LATVIA	
Longidorus elongatus	(Eglitis et al., 1962; Peterson and Kilevitis, 1968)
MOLDAVIA	
Longidorus elongatus	(Koev and Nesterov, 1974; Koev and Polinkovskii, 1977; Koev et al., 1971; Kozhokaru, 1968; Polinkovskii, 1979; Stegarescu, 1972)
sylphus	(Polinkovskii, 1979)
vineacola	(Lisetskaya, 1968, 1971; Polinskovskii, 1979)
Xiphinema americanum	(Dementeva, 1968; Koev and Nesterov, 1974; Koev and Polinskovskii, 1976, 1977;Koev et al., 1970, 1971; Lisetskaya, 1968; Nesterov and Lisetskaya, 1967; Polinskovskii, 1979; Stegarescu, 1966, 1972)
diversicaudatum	(Polinskovskii, 1979; Stegarescu, 1966, 1972)
index	(Fritzsche and Thiele, 1979; Koev and Nesterov, 1974; Koev and Polinskovskii, 1976, 1977; Koev et al., 1971; Polinskovskii, 1979; Stegarescu, 1962, 1968, 1972)
italiae	(Polinskovskii, 1979)
pachtaicum	(Polinskovskii, 1979; Stegarescu, 1972)
turcicum	(Polinskovskii, 1979; Stegarescu, 1967, 1972)
vuittenezi	(Koev and Polinskovskii, 1977; Kozhokaru and Korolchuk, 1976; Polinskovskii, 1979; Stegarescu, 1972)

TABLE 8 : continued

TADZHIKSKAYA	
Longidorus africanus	(Ivanova, 1972; Ivanova and Kankina, 1972)
elongatus	(Ivanova, 1972)
tardicauda	(Ivanova, 1972, Ivanova and Kankina, 1972)
Xiphinema americanum	(Ivanova, 1972; Ivanova and Kankina, 1972)
index	(Ivanova, 1972; Ivanova and Kankina, 1972; Kankina, 1978)
pachtaicum	(Kankina, 1978)
TURKMENSKAYA	
Xiphinema americanum	(Kiryanova and Shagalina, 1969, 1974)
index	(Kiryanova and Shagalina, 1969, 1974)
UKRAINE	
Longidorus elongatus	(Milkus et al., 1974)
Xiphinema americanum	(Milkus et al., 1974, 1975)
diversicaudatum	(Milkus et al., 1974, 1975)
index	(Milkus, 1976; Milkus et al., 1974)
vuittenezi	(Milkus et al., 1974, 1975)
UZBEKSKAYA	
Longidorus elongatus	(Kiryanova, 1951)
Paralongidorus georgiensis	(Tulaganov, 1937)
nudus	(Kiryanova, 1951)
Xiphinema index	(Azizova, 1970)
pachtaicum	(Tulaganov, 1938, 1949)

CHAPTER IV

THE DISTRIBUTION OF XIPHINEMA DIVERSICAUDATUM

IV : 1 EUROPEAN DISTRIBUTION

Micoletzky (1923) identified one eggless female nematode, obtained from alluvium from the river Volga, USSR, as Dorylaimus (Longidorus) elongatus. However, Micoletzky (1927) included this specimen with two male and one juvenile specimen, obtained from alluvium dredged from the rivers Obwa and Wjatka near to where they join the river Kama, USSR, and used them to describe Dorylaimus (Sg. Longidorus) diversicaudatus nov. spec. Thorne and Swanger (1936) raised the subgenus Longidorus to generic level thus Micoletzky's (1927) species became Longidorus diversicaudatus. Thorne (1939), in his monograph of the Dorylaimoidea, transferred the species to the Xiphinema genus and altered the specific name to X. diversicaudatum to make it comply with the correct gender for the

genus. However, Thorne (1939) gives a misleading figure when describing X. diversicaudatum and probably included more than one species (see IV:2:8).

Dorylaimus cateri var. parvus f. rotundatus sf. diversicaudatus (Micoletzky, 1922) was believed by Franz (1942) to be X. diversicaudatum but this species is synonymous with Eudorylaimus junctus (Andrassy, 1959). Also Alther (1958) originally described X. paraelongatum but Luc and Tarjan (1963) subsequently synonymised this species with X. diversicaudatum. X. diversicaudatum was redescribed by Goodey et al (1960) and subsequently by Pitcher et al (1974) who also designated a new lectotype male specimen and confirmed the presence of a Z-pseudo-organ in the genital branches of females.

In Europe X. diversicaudatum has been reported from every country except Finland and Romania; it is probably present in the latter country, but has yet to be found or identified from it. The species appears to favour the northern European countries from which it is most frequently recorded. It is also recorded from the northerly parts of southern European countries, but rarely in the southerly parts. It would therefore seem that the most favourable conditions for the survival of this species are present in England, Wales, northern France, Belgium, The Netherlands, northern Italy and east and west Germany.

The most southerly European record of X. diversicaudatum is reported from the Greek Island of Kos where a small population was found in soil samples collected in a vineyard. Several morphometrics of eight female and three male specimens and photomicrographs of the posterior end of a male and female specimen and of the anterior end of a specimen are given by Terlidou (1967). The vineyard still exists,

from which the original specimens were collected, and was resampled in 1980 in an attempt to obtain specimens for the present study. However, only X. index and X. pachtaicum were present in the resampled soils which were collected by Mr Vlachopoulos and Mrs Gazella, Institute of Phytopathology, Benaki, Greece. The original population of X. diversicaudatum from this biotope apparently consisted of only a few individuals therefore it is possible that the species was not relocated as insufficient soil samples were taken during the resampling. Alternatively, the species may not have survived at this biotope.

X. diversicaudatum is considered to be a species complex in Italy and in the valley of a tributary of the river Po the species has been found only in soils at an altitude greater than 300 metres whereas X. index was found only in soils below this altitude. X. vuittenezi was associated with both X. diversicaudatum and X. index at these sites (F. Lamberti, pers. comm.). In England X. diversicaudatum was reported to be mostly associated with silt and clay soils and in hedgerows (Harrison and Winslow, 1961) but Taylor and Brown (1976) subsequently reported the species from a wide range of plants growing in many soil types, including the lighter sandy loams and loamy sands. Also, X. diversicaudatum has been identified from peaty soils in The Netherlands (J. W. Seinhorst, pers. comm.), and in West Germany in natural habitats, X. diversicaudatum has been found in soils overlying Cretaceous chalk but was not present in soil from above underlying Jurrasic chalk (Rau, 1975).

IV : 1 : 1 Xiphinema israeliae n. sp. from Israel

X. diversicaudatum was reported, in several publications, to be present in Israel (Cohn, 1969; Cohn and Mordechai, 1969, 1970; Cohn and Sher, 1972; Cohn et al., 1973). The original specimens from Israel were found to have morphometrics which fitted within the

relatively broad range of measurements of X. diversicaudatum as redescribed by Goodey et al., (1960). During subsequent years additional Xiphinema spp. with pegged tails were described and the descriptions contained much detail of the nematodes morphology, particularly of the female reproductive system. Flegg (1966) reported the presence of a Z-organ in the female genital tracts in some English populations of X. diversicaudatum and Luc and Dalmasso (1975) later described the character as a pseudo-Z-organ. However, as none of these populations was from the type locality X. diversicaudatum was not considered by Cohn and Sher (1972), to have a 'Z-organ' present. Pitcher et al. (1974) subsequently confirmed the presence of 'Z-organs' in females of several European populations of X. diversicaudatum.

Specimens of 'X. diversicaudatum' to be used for the present study, were obtained from lemon (Citrus medica limonum) from Tel Mond, Israel via Professor E. Cohn, Israel. Examination of these specimens revealed that females did not have a pseudo-Z-organ. Also, the morphometrics obtained from the specimens were generally smaller than those obtained from other populations of X. diversicaudatum. Therefore, it was concluded that the X. diversicaudatum from Israel was probably a new species.

Concurrently, but independent of the present study, Dr M. Luc, Paris had made similar observations and had also reached the conclusion that the specimens from Israel represented a new, undescribed, species. The results obtained from this study were combined with those obtained by Dr M. Luc and a taxonomic description of X. israeliae n. sp. has been published (Luc et al., 1982).

IV : 2 DISTRIBUTION OUTWITH EUROPE

X. diversicaudatum has been reported from several countries

outwith Europe and it was presumably transported to these other areas, from Europe, in soil associated with planting material. The countries outwith Europe in which X. diversicaudatum has been recorded are listed alphabetically.

IV : 2 : 1 Australia

X. diversicaudatum has been reported from two states in Australia. In Victoria, Stubbs (1971) reported X. diversicaudatum associated with severely diseased roses in one of Melbourne's public gardens and from a garden at the Department of Agriculture Plant Research Institute, Burnley. However, the original samples were collected in 1964 and since then the gardens have been replaced with turf and it is not known if X. diversicaudatum is still present at these two sites (R. H. Brown, in litt.).

Colbran (1964), in a list of nematode species and their associated host plants found in Queensland, includes three entries with X. diversicaudatum. The original samples were collected in the early 1960's and after re-examining the original specimens, collected at that time, Colbran (in litt.) considers that the specimens should probably be referred to X. basiri.

Therefore it is concluded that X. diversicaudatum may not, any longer, exist in Australia and if it does, is probably rare. Also the original identification from Victoria needs to be verified as these specimens, originally obtained from the two gardens, may be another species - like the specimens from Queensland.

IV : 2 : 2 Canada

Townshend (1961) reported X. diversicaudatum associated with glasshouse grown roses in Ontario, Canada. Recent resampling has failed to locate this species and the use of a sterilant nematicide,

dbromochloropropane (DBCP), has possibly eradicated it from these sites (Townshend, in litt.).

IV : 2 : 3 Equatorial Guinea

Luc (1958) and Luc and De Guiran (1960) reported X. diversicaudatum in soil from the rhizospheres of Cinchona ledgeriana Moens. and Oryza sativa L. both from Seredou, Equatorial Guinea, West Africa. The identification of the specimens from these biotopes was based on Thorne's (1939) description of X. diversicaudatum before the redescription of X. diversicaudatum by Goodey et al. (1960) was available. Because of the errors, reported by Goodey et al. (1960), in Thorne's (1939) description of X. diversicaudatum the specimens from the two sites in Equatorial Guinea were re-examined. This has resulted in the specimens being described by Luc (1975) as a new Xiphinema species, X. seredouense. Therefore, X. diversicaudatum has not been recorded in Equatorial Guinea.

IV : 2 : 4 Guam

Reinking and Radewald (1961) reported X. americanum and X. diversicaudatum associated with coconut trees (Cocus nucifera) particularly coconut trees affected by yellow mottle decline (Cadang-Cadang disease). No agency on Guam appears to have any records of the original work done by the late Dr Reinking and the only information available is that the original research area was probably in the southern portion of Guam near Merizo (G. Beaver, in litt.). Specimens of the original material examined are not available (Radewald, in litt.). Therefore, with the absence of original material and the original localities no longer identifiable from which new specimens could be obtained, it is concluded that the original identification should be considered an identification inquirendae.

Also, with the descriptions of many new Xiphinema species since 1961 (Fig. 2) it is possible that the specimens originally identified as X. diversicaudatum would now be referred to a different species.

IV : 2 : 5 Java

Although X. diversicaudatum has never been reported from Java specimens of a Xiphinema sp. were received for identification during the present study. The specimens were extracted from soil collected from around the roots of stunted and chlorotic Zea mays L. at K.P. Segunung, West Java, but the damage to the Z. mays was not necessarily caused by the Xiphinema sp.

The specimens were identified as X. vulgare, a species which had previously been reported from Java (Tarjan, 1964) and the juvenile stages present were used to prepare a description of these stages (Brown et al, 1981) as this information was absent in other descriptions of the species.

IV : 2 : 6 Malawi

X. diversicaudatum has not been reported from Malawi but Saka and Siddiqi (1979) reported the presence of X. coxi. Therefore, as X. diversicaudatum and X. coxi have several morphological similarities in common, specimens of Xiphinema spp. were obtained from several of the original sites from which X. coxi had been identified.

Although several Xiphinema species were identified from soil samples collected from the five sites which were resampled, X. coxi was absent from all of them. The species present were X. michelluci and L. pisi from sugar cane from Nchalo; X. elongatum, X. limbeense n. sp. and X. malawasi n. sp. from grapefruit (Citrus paradisi) from Bvumbwe; X. basilgoodeyi and X. elongatum from peach (Prunus persica) from Bvumbwe; X. elongatum from paw paw

(Carica papaya) from Bvumbwe and X. basilgoodeyi and X. elongatum from Pinus sp. from Bvumbwe. Several morphometrics of these species from each biotope are presented in Tables 9, 10,11 and 12.

The only Longidorus specimens present in the samples were L. pisi from sugar cane from Nchalo and one of the specimens was a male. As a male L. pisi has not previously been described a full description has been published (Brown et al., 1982).

Siddiqi (1979), in the original description of the species, reported the presence of many spine-like bodies in the tubular portion of the uteri of X. michelluci. He thought they were spores of a parasite. Similar inclusions were observed in the uteri of the female specimen from Nchalo. An alternative to Siddiqi's (1979) suggestion is that the inclusions in the uteri of X. michelluci may be an integral part of the reproductive system of X. michelluci and have a similar function to the uterine spines present in X. rarum and X. spinuterus and the uterine stellate spines present in X. mammatum (Luc, 1979). However, further study is required to precisely determine the nature of the uterine inclusions in X. michelluci.

Specimens of Xiphinema spp., although generally similar to X. coxi, mainly differed from X. coxi by having much shorter body lengths and a pseudo-Z-organ containing rounded apophyses compared with angular apophyses present in X. coxi. The Xiphinema spp. were the subject of a joint study with Dr M. Luc, France and two new species X. limbeense n. sp. and X. malawiense n. sp. were fully described at the conclusion of the study (Brown et al., 1983).

IV : 2 : 7 New Zealand

X. diversicaudatum was originally identified in New Zealand from soil from the rhizosphere of Cyphomandra betacea Sendt. at Te Puke and from apple at Riverhead (Dale, 1971). Dale (1972) subsequently

listed several host plants for X. diversicaudatum in New Zealand and Thomas and Procter (1972) reported X. diversicaudatum transmitting arabis mosaic virus to C. betacea at two properties at Te Puke.

The original C. betacea and apple orchard sites were resampled during 1978 but X. diversicaudatum was not found. However, a large population of X. diversicaudatum was found at a peach orchard at Alexandra and a much smaller population was found associated with virus - diseased celery at Christchurch. Subsequently, the peach orchard has been flooded as part of a major Hydro-Electric Power Scheme (C. J. Barber, in litt.).

It seems that X. diversicaudatum is relatively rare in New Zealand and is represented only by a few, sporadically distributed populations.

IV : 2 : 8 United States of America

One of the earliest records of X. diversicaudatum in the USA was given by Thorne (1939) who reported it from the states of Virginia and Utah. However, it is suspected that Thorne was probably dealing with two species of Xiphinema. Thorne (1939) stated that the X. diversicaudatum specimens from Utah "were practically identical (with type specimens from the USSR) except for their slightly longer, more robust, tails" and Thorne (1961) later stated that he used these specimens to emend the original description. However, the drawings of X. diversicaudatum presented by Thorne (1939) were made from specimens from Virginia and if these specimens are of a different species this could explain why they differed from the figures of the type specimens as presented by Micoletzky (1923, 1927). Goodey et al. (1960), who noted the apparent differences in tail shape in the figures of Thorne and Micoletzky also noted the values for magnification given by Thorne (1939) were incorrect and that in a drawing of the anterior end of a

specimen two basal rings were included for the guiding sheath. Therefore, Thorne (1939) possibly identified X. diversicaudatum only from Utah and the specimens from Virginia probably refer to another Xiphinema species.

Thorne (1939) correctly reported that X. diversicaudatum was described by Micoletzky (1923, 1927) from specimens from the USSR. But Thorne (1961) subsequently incorrectly reported that the specimens came from soil found in Austria. Micoletzky was Austrian and Thorne probably confused the author's birthplace with the country of origin of the type specimens of X. diversicaudatum.

Schindler (1954) reported X. diversicaudatum in association with root galling of greenhouse grown roses in northeastern USA and a survey of commercial greenhouses in 14 states of the USA demonstrated that Xiphinema spp., including X. diversicaudatum, were common in most areas (Schindler, 1956). Using a population of X. diversicaudatum obtained from a commercial rose-growing greenhouse in Indiana, Schindler (1957) and Schindler and Braun (1957) demonstrated the parasitism and pathogenicity of X. diversicaudatum to several crop plant species.

Schindler and Henneberry (1962) suggested methods for controlling nematodes in outdoor rose plantings by using sterilant nematicides such as DBCP. The implementation of these control measures appears to have helped eradicate X. diversicaudatum from rose-growing greenhouses in the northeastern USA as nematologists in the eastern USA have no records of its presence.

X. diversicaudatum has been reported from California (Pitcher et al., 1973) where it was found at two residential properties, in 1970, during a regular urban detection programme. Also, in 1975 the

species was found in soil from the rhizosphere of roses growing in a greenhouse. All three sites were treated with a soil-sterilant and X. diversicaudatum has not been found in soil samples subsequently taken from one of the urban sites and from the greenhouse. However, despite repeated use of soil-sterilants small numbers of X. diversicaudatum have still been recovered from soil samples taken from the remaining urban site at San Diego (K. F. Sims, in litt.).

Riffle (1968) identified X. diversicaudatum amongst 30 other genera and species, from soil taken from the rhizosphere of stands of Pinus ponderosa L. at Corona, Manzano and Tajique, New Mexico. Also, P. ponderosa was identified as an excellent host for X. diversicaudatum (Riffle, 1970).

During the present study it was not possible to obtain a culture of X. diversicaudatum from New Mexico but Dr J. Riffle, USA kindly supplied three slides, containing specimens that he had originally identified as X. diversicaudatum. Riffle (in litt.) disclosed that Dr R.T. Robbins, USA compared specimens of X. diversicaudatum from New Mexico with specimens of the species deposited in the nematode collection at the University of California, Davis. Robbins concluded that the specimens from New Mexico were not X. diversicaudatum and that they represented an undescribed species. Riffle, after further observation of the specimens from New Mexico, concurred with Robbins. This new information has not been published and thus the original report of X. diversicaudatum present in New Mexico has never been corrected.

Morphometrics from male and female specimens of 'X. diversicaudatum' from New Mexico, contained on slides supplied by Dr J. Riffle, are given in Tables 13 and 14. X. diversicaudatum from New Mexico was identified as being morphologically and

morphometrically similar to X. sahelense and morphometrics from populations of X. sahelense described from Algeria and Portugal (Dalmasso, 1969; Macara, 1970) are also given in Tables 13 and 14 for comparative purposes. It is concluded that X. diversicaudatum in Riffle 1968 and 1970 and Anon, 1971 should be referred to X. sahelense.

Outwith Europe X. sahelense has been reported only from a few biotopes in Malawi (Saka and Siddiqi, 1979). In Europe X. sahelense has been reported from Spain (Arias, 1979), from grapevine in Algeria (Dalmasso, 1969) and from several hosts, particularly woody perennials including Pinus spp., in Portugal. Therefore, it is possible that as with X. index, which is considered to have been introduced to several areas of the world in soil associated with planting material, X. sahelense similarly was introduced to New Mexico with planting material transported there by Portugese or Spanish immigrants.

IV : 3 CONCLUSIONS

X. diversicaudatum is present in almost every European country but is absent from all North African countries. The species is widespread in many of the northern European countries although in several of them it appears to be mainly restricted to particular areas, e.g. northern Italy. In the western states of the USSR X. diversicaudatum appears to be relatively common and, as in most European countries, it is frequently found associated with arabis mosaic or strawberry latent ringspot viruses which it transmits.

Outwith Europe, X. diversicaudatum has been reported from Australia, Canada, Guam, New Zealand and the USA and was usually associated with Rosa sp. However, it appears unlikely that X. diversicaudatum has survived in Australia and Canada and is probably only present at a very few scattered localities in the USA

and New Zealand. Also, the report of X. diversicaudatum from Guam is considered to refer to another species.

IV : 4 ADDENDUM

Specimens of X. diversicaudatum were received during March 1983 from Professor J. Heyns, Rand Afrikaans University, Johannesburg, South Africa. The nematodes, which had originally been collected by Dr. P. Smith from the rhizosphere of peach trees (Prunus persica) from the South Western Cape area, South Africa, are generally smaller than the type specimens of X. diversicaudatum. However, the morphometrics obtained from the South African specimens overlap with those obtained from other populations examined as part of the present study.

Information about the specimens of X. diversicaudatum from South Africa will be the subject of a publication by Professor Heyns, therefore no details are given in this report.

TABLE 9 : Morphometrics of X. michelluci and L. pisi from sugar cane from Nchalo, Malawi.

		X. michelluci	L. pisi	
		1 female	1 male	12 females
L	mm	3.76	2.47	2.7 ± 0.15* (2.5 - 3)
a		58	88	94 ± 5 (88 - 104)
b		8.7	8.4	12 ± 2.2 (8.8 - 14.4)
c		52.2	118	73 ± 6.5 (66 - 82)
c'		1.54	1.33	2 ± 0.16 (1.8 - 2.3)
V	%	48.4	-	48 ± 1.5 (45 - 50)
Odontostyle	u	121	70	66 ± 3 (60 - 69)
Odontophore	u	70	32	39 ± 2.9 (33 - 43)
Spear	u	191	102	104 ± 3.4 (99 - 108)
Body width greatest	u	65	28	29 ± 1.9 (25 - 31)
Body width at anus	u	47	21	19 ± 1 (17 - 21)
Body width at spear base	u	49	23	22 ± 1.1 (21 - 24)
Tail length	u	72	28	38 ± 2.5 (32 - 40)
Anterior to oesoph/ intest junction	u	433	293	234 ± 39 (198 - 300)
Spicula	u	-	34	-

*, Mean ± one standard deviation (n - 1) and range

TABLE 10 : Morphometrics of X. elongatum, X. limbeense n. sp. and X. malawiense n. sp. from citrus from Bvumbwe, Malawi.

		X. elongatum	X. limbeense	X. malawiense
		2 females	11 females	14 females
L	mm	1.75* (1.56 - 1.94)	2.5 + 0.1** (2.44 - 2.81)	2.65 + 0.14** (2.44 - 2.94)
a		49	58 + 4.9 (49 - 68)	52 + 4.6 (46 - 64)
b		4.15 (4.11 - 4.18)	6.8 + 0.25 (6.5 - 7.2)	6.8 + 0.47 (6.3 - 7.9)
c		29.5 (29 - 30)	42 + 2.6 (35 - 45)	57 + 7.3 (44 -67)
c'		2.52 (2.36 - 2.68)	2.22 + 0.18 (1.81 - 2.44)	1.5 + 0.24 (1.21 - 2.03)
V	%	48.5 (48 - 49)	42 + 1.3 (41 - 45)	44 + 1.9 (40 - 46)
Odontostyle	u	86 (85 - 87)	95 + 2.4 (90 - 97)	111 + 3.3 (103 - 117)
Odontophore	u	59 (55 - 63)	69 + 2.7 (65 - 74)	75 + 1.6 (72 - 76)
Spear	u	145 (142 - 148)	164 + 2.5 (160 - 167)	186 + 4.1 (175 - 193)
Body width greatest	u	36 (32 - 40)	44 + 3.9 (36 - 52)	51 + 5.4 (43 - 59)
Body width at anus	u	23.5 (22 - 25)	27 + 1.9 (26 - 32)	32 + 2.2 (29 - 37)
Tail length	u	59.5 (52 - 67)	61 + 4.1 (57 - 71)	47 + 5.8 (41 - 63)
Anterior to oesoph/ intest junction	u	391.5 (380 - 403)	374 + 19 (346 - 410)	389 + 19 (346 - 419)
Anterior to vulva	mm	1.69 (1.51 - 1.87)	1.09 + 0.05 (1.06 - 1.19)	1.18 + 0.08 (1.06 - 1.31)

*, Mean and range
**, Mean ± one standard deviation (n - 1) and range

TABLE 11 : Morphometrics* of X. basilgoodeyi and X. elongatum from peach from Bvumbwe, Malawi.

		X. basilgoodeyi		X. elongatum
		3 males	3 females	2 females
L	mm	2.68 (2.61 - 2.71)	2.78 (2.72 - 2.82)	2.34 (2.31 - 2.36)
a		56 (53 - 60)	56 (55 - 57)	59
b		7.8 (6.7 - 8.7)	7.2 (6.7 - 8.2)	6.78 (6.13 - 7.43)
c		55 (53 - 57)	60 (56 - 66)	33 (32 - 34)
c'		1.24 (1.17 - 1.31)	1.31 (1.28 - 1.33)	2.89 (2.61 - 3.17)
V	%	-	45 (43 - 49)	40 (39 - 41)
Odontostyle	u	107 (103 - 111)	107 (105 - 111)	89
Odontophore	u	69 (68 - 72)	75 (72 - 78)	63 (61 - 65)
Spear	u	176 (171 - 183)	182 (177 - 186)	152 (150 - 154)
Body width greatest	u	48 (44 - 51)	50 (49 - 51)	39.5 (39 - 40)
Body width at anus	u	39 (39 - 40)	36 (33 - 37)	24.5 (23 - 26)
Tail length	u	49 (47 - 51)	47 (43 - 49)	71 (68 - 74)
Anterior to oesoph/ intest junction		348 (311 - 402)	391 (333 - 421)	347.5 (318 - 377)

*, Mean and range.

TABLE 12 : Morphometrics of X. elongatum from paw paw and Pinus sp. and X. basilgoodeyi from Pinus sp. from Bvumbwe, Malawi.

		X. elongatum		X. basilgoodeyi
		paw paw	Pinus sp.	
		9 females	6 females	1 female
L	mm	2.43 ± 0.12*	2.36 ± 0.12	2.77
		(2.24 - 2.60)	(2.17 - 2.46)	
a		61 ± 3.9	61 ± 4.4	58
		(55 - 67)	(54 - 67)	
b		7.2 ± 0.52	7.1 ± 0.38	7.3
		(6.2 - 8)	(6.4 - 7.4)	
c'		2.63 ± 0.16	2.45 ± 0.16	1.3
		(2.39 - 2.91)	(2.28 - 2.67)	
V	%	38 ± 1.1	38 ± 1	44
		(37 - 40)	(37 - 40)	
Odontostyle	u	90 ± 6.2	92 ± 4.4	106
		(77 - 94)	(89 - 101)	
Odontophore	u	59 ± 2.3	61 ± 4.4	73
		(57 - 64)	(52 - 64)	
Spear	u	149 ± 6.8	153 ± 1.2	179
		(133 - 155)	(151 - 154)	
Body width greatest	u	40 ± 3.3	39 ± 3.1	48
		(35 - 45)	(35 - 42)	
Body at anus	u	25 ± 1.5	25 ± 0.52	35
		(22 - 27)	(25 - 26)	
Tail length	u	65 ± 5.7	62 ± 3.9	46
		(53 - 72)	(57 - 69)	
Anterior to oesoph/ intest junction	u	339 ± 23.3	332 ± 7.5	379
		(308 - 389)	(320 - 339)	

*, Mean ± one standard deviation (n - 1) and range

TABLE 13 : Morphometrics* of female X. sahelense from New Mexico, USA, Algeria and Portugal.

		New Mexico	Algeria	Portugal
n		7	24	10
L	mm	3.95 ± 0.18 (3.81 - 4.31)	4.41 (3.77 - 4.91)	3.81 (3.34 - 4.19)
a		73 ± 5.1 (67 - 81)	78 (69 - 89)	66 (56 - 79)
b		8.9 ± 1.1 (7.9 - 11)	8.8 (7.5 - 9.8)	8.8 (7.6 - 9.6)
c		71 ± 8.2 (61 - 81)	83 (73 - 92)	86 (73 - 96)
c'		1.4 ± 0.2 (1.1 - 1.7)	1.5 (1.4 - 1.6)	1.2 (1 - 1.6)
V	%	46 ± 3.5 (42 - 52)	46 (45 - 58)	44 (40 - 47)
Odontostyle	u	111 ± 2.2 (108 - 113)	130 (124 - 137)	126 (124 - 130)
Odontophore	u	66 ± 4.3 (61 - 74)	78 (74 - 80)	70 (66 - 76)
Spear	u	178 ± 5.1 (171 - 186)	207 (199 - 213)	na
Body width greatest	u	55 ± 3.7 (47 - 59)	57 (43 - 64)	na
Body width at anus	u	39 ± 2.1 (36 - 41)	36 (31 - 41)	38 (34 - 48)
Tail	u	56 ± 8 (47 - 67)	54 (48 - 60)	45 (40 - 54)
Anterior to oesoph/ intest junction	u	447 ± 30 (391 - 483)	499 (425 - 578)	na

*, Mean and range, also one standard deviation (n - 1) given for the population from New Mexico.
na, Not available

TABLE 14 : Morphometrics* of male X. sahelense from New Mexico, USA, Algeria and Portugal.

		New Mexico	Algeria	Portugal
n		1	40	12
L	mm	4.44	4.23 (3.93 - 4.79)	3.91 (3.35 - 4.35)
a		85	88 (77 - 101)	71 (60 - 91)
b		11	8.7 (7.7 - 10.2)	9.1 (7.7 - 10.6)
c		85	82 (75 - 87)	92 (80 - 103)
c'		1.4	1.44 (1.31 - 1.57)	1.2 (1 - 1.5)
Odontostyle	u	112	128 (112 - 133)	132 (124 - 140)
Odontophore	u	70	74 (66 - 82)	67 (62 -72)
Spear	u	182	201 (193 - 207)	199 (188 - 212)
Body width greatest	u	52	51 (42 - 58)	na
Body width at anus	u	38	37 (33 - 42)	35 (32 - 41)
Tail	u	52	52 (46 - 60)	43 (37 - 48)
Anterior to oesoph/ intest junction	u	403	500 (436 - 553)	na

*, Mean and range.
na, Not available.

PART TWO

"MORPHOMETRIC VARIABILITY"

CHAPTER V

MORPHOMETRIC VARIABILITY IN NEMATODES

V : 1 INTRODUCTION

Morphometric differences occurring between populations of a nematode species or between specimens of a nematode population have been reported by many research workers. The differences have been reported to be geographical, ecophenotypic or host induced (Goodey, 1952; Rohde and Jenkins, 1957; Bird and Mai, 1965; Fisher, 1965; De Grisse and Loof, 1970; Azmi and Jairajpuri, 1976; Tarte and Mai, 1976; Evans and Franco, 1977; Tarjan and Frederick, 1978). Coomans (1962) reported that the morphometric ratios a and b had a wide range of variability in Rotylenchus goodeyi. Morphometric and allometric variations between populations of Trichodorus christiei were reported to be influenced more by host than geographical origin (Bird, 1966) and in the same species spear length and the ratio V were least variable whereas ratios G1 and G2 were most variable (Bird and Mai, 1967). Jairajpuri (1969) reported morphological differences occurring in specimens of Parahadronchus shakili from different localities and habitats and also in specimens from the same popu lation. Specimens of Helicotylenchus indicus from one population, had least variation recorded in head height, vulva position, ratios V, G1 and a in adults; median bulb, excretory pore and ratios O and c in juveniles whilst much variation was recorded in several other characters (Azmi and Jairajpuri, 1976). Tarte and Mai (1976) used a population of Pratylenchus penetrans, originating from one gravid female, to study

morphological variation. The variability in the population of P. penetrans studied by these research workers was sufficiently great to make them suggest that several other Pratylenchus species could be conspecific with P. penetrans.

V : 2 MORPHOMETRIC VARIABILITY IN THE LONGIDOROIDEA

In common with nematodes in other genera, morphometric variability has been reported for several species in the Longidoroidea. Lima (1965) reported morphometric variability in X. americanum and based on a study of 25 morphological characters he suggested that X. americanum was not a single species but a complex of at least seven distinct species. Tarjan (1969) rejected most of Lima's (1965) proposals and concluded that the X. americanum group comprised only four closely related species "and a collection of geographical variants that exhibit basic similarities despite some divergent morphological features". The X. americanum complex was re-examined by Lamberti and Bleve-Zacheo (1979) and they concluded "We prefer to recognise a group (= X. americanum group) of 25 species with characters typical of the genus Xiphinema, Cobb, 1913 as originally described". They described 15 new species from examinations of mounted specimens identified as others by X. americanum sensu lato.

Morphological variation has been reported for other longidoroid nematodes. Body width, oesophageal and tail lengths of Xiphinema and Longidorus species exhibit negative allometric growth with body length (Sturhan, 1963c). Differences in body length, ratios a, b and c' and posterior gonad length were reported to occur in populations of X. bakeri from northwestern and southeastern USA (Tarjan, 1964). Heyns (1974a and b) correlated intraspecific variations in X. brevicolle and X. elongatum with the geographical location of the different populations. Variability in populations of X. insigne from

India was used by Bajaj and Jairajpuri (1977) to group the populations into X. indicum-forms and X. insigne-forms. Loof and Maas (1972) reported intraspecific variation in populations of Xiphinema species from Surinam and concluded that body dimensions alone were unsatisfactory for distinguishing species and that qualitative characters should also be given at least equal taxonomic weightings. Tail shape showed the most variability between populations of X. krugi (Frederick and Tarjan, 1974) and odontostyle length and ratio V were the least variable characters observed in specimens of X. basiri from one population (Bajaj and Jairajpuri, 1977). Odontostyle length, tail length, body width and distance from the anterior to the guide ring were about 15% larger in populations of L. elongatus without males than in populations with males (Kozlowska and Seinhorst, 1979). Martelli et al. (1966) reported that much morphometric variability was evident within and between populations of X. italiae. And, the biotopes at which X. italiae occurred appeared to influence the nematodes morphometrics.

V : 3 MORPHOMETRIC VARIABILITY IN X. DIVERSICAUDATUM.

Since the description of X. diversicaudatum by Micoletzky (1927), morphometrics of adults from different populations have been reported by several authors, including a redescription of the species (Goodey et al., 1960; Erbenova, 1975; Hrzic, 1978; Martelli and Lamberti, 1967; Szczygiel, 1974; Teploukhova, 1974; Terlidou, 1967). The morphometrical variability existing between populations of X. diversicaudatum recorded in these reports may be due to biogeographical factors affecting the various populations or may be the result of misidentification of the species by some authors. However, if the identifications are assumed to be correct much variability is present between populations and this may account for reports of "large" and "small" X. diversicaudatum in England

(Weischer, 1964).

The morphometrical variability apparent between several different populations of X. diversicaudatum, as reported in a number of publications, is given in Tables 15 and 16. The percentage difference between the largest and smallest values, for each structure measured or ratio (Tabs. 15 and 16) are presented in Table 17.

In selecting the data for Tables 15 and 16 three publications containing data were rejected. Thorne (1939) presents the morphometrics reported by Micoletzky (1927) but the drawings of specimens presented by Thorne (1939) are probably of a different Xiphinema sp. therefore no measurements were taken from these drawings. Thorne (1961) presents some morphometrics but it is not known if the values given refer only to X. diversicaudatum or if they include data obtained from specimens obtained from Virginia which were not X. diversicaudatum. Esser (1973) presented morphometrics of X. diversicaudatum but the values were taken from Goodey et al. (1960), Sturhan (1963b) and Thorne (1939). Also the tail shape illustrated by Esser (1973) was taken from Thorne (1939) and therefore does not represent the correct tail shape of X. diversicaudatum. Repetition of data (data in Tables 16 and 17 were obtained only from copies of the original papers) is also contained in several publications, e.g. Goodey et al. (1960) includes Micoletzky's (1923, 1927) original data; Martelli and Lamberti (1967) include Goodey et al's. (1960) data obtained from English specimens; Pitcher et al. (1974) also include these latter data and Micoletzky's (1923, 1927) data; Terlidou (1967) includes some of the original data reported by Thorne (1961) and Erbenova (1975) includes data reported in Martelli and Lamberti (1967), some of which were originally reported by Goodey et al. (1960).

To make Tables 15 and 16 as comprehensive as possible some values were derived from the published data, e.g. the value of 42 u for tail length for population A was obtained by dividing the published values of L by ratio c. Also, some data were calculated from direct measurements made from drawings of specimens presented in the various publications. Values derived from published data or from measurements of drawings are indicated in the Tables.

Much variability is apparent between the populations of X. diversicaudatum also the degree of variability, in itself, varies between the different structures and ratios measured. The smallest reported mean body length for female specimens was from a Greek population of X. diversicaudatum (Terlidou, 1967) and this value was 27% less than the largest reported mean body length (4.9 mm) from an English population (Goodey et al., 1960). The smallest percentage differences between reported means of morphometrics for female specimens were those recorded for the lengths of the odontostyle, odontophore and spear. Similarly, for male specimens the smallest percentage differences were recorded for the length of the odontostyle and the ratio T. Generally, the largest differences between means of morphometrics, for both male and female specimens, were recorded for the greatest body width and the body width at the anus. However, the large differences in body widths are partly caused by values derived from morphometrics, reported by Martelli and Lamberti (1967), of West German specimens of X. diversicaudatum. Martelli and Lamberti (1967) present values for body length and ratios a, c and c' and these values were used to calculate values for greatest body width and body width at the anus. However, the values for ratios a (body length divided by greatest body width) reported by Martelli and Lamberti (1967) are much smaller than values for ratio a given in other reports. Therefore, it

is possible that the specimens measured by Martelli and Lamberti (1967) were somewhat flattened creating a disproportionately large value for the greatest body width compared with body length. Alternatively, the specimens examined by Martelli and Lamberti (1967) may represent a Xiphinema species different from X. diversicaudatum.

The percentage differences in the means of the 12 measurements and ratios for females of X. diversicaudatum from different populations (Tab. 17) ranged from 9% for odontostyle length to 49% for body width at the anus and the average percentage difference for all 12 parameters measured was 24%. Similarly, for male X. diversicaudatum the percentage differences in the means ranged from 7% for ratio T to 39% for body width at the anus and the average percentage difference for all 13 parameters measured was 20%. Therefore, a comparison of the published morphometrics of different populations of X. diversicaudatum shows that, in general, there is a variability in the measurements of 20% to 25%.

The apparent variability existing between the populations of X. diversicaudatim, as shown above, cannot be attributed to any one factor. Intrinsic factors necessary for the survival of a nematode population at a particular biotope such as host, altitude, rainfall, temperature and soil structure have been cited, in other reports, to be related to morphometric variability in plant nematodes. Also, several extrinsic factors such as the effect of the operator recording the measurements, the measuring system employed and procedures adopted for killing, fixing and mounting specimens in glycerol also themselves may be a cause of morphometric variability. These latter factors may be especially important when comparing published data recorded by different workers in different institutions.

TABLE 15 : Published means of morphometrics of female X. diversicaudatum from different populations.

		X. diversicaudatum										
	♀	A	B	C	D	E	F	G	H	I	J	K
n		1	5	na	43	8	11	5	1	19	5	6
L	mm	4	4.4	4.4	4.9	3.6*	4.03	4.2	4.6	4.2	4.5	4.5
a		72	78	76	74	66*	70	68	54	73	71	65
b		10.1	9	8.2	9.1	8.9*	8.9	8.3	9.1	8.2	9	8.9
c		96	85	88	78	87*	94	90	83	88	97	100
c'		1.1	na	0.9*	1*	1.3+	1.2	1.1*	0.8	na	1.1	0.9
V	%	48	46	43	43	43*	43	45	39	43	45	44
Odontostyle	u	133	132	140	143	na	133	131	146	137	142	134
Odontophore	u	78	na	82	85	na	80	86	87	83	83	82
Spear	u	211+	na	222	228	na	212	217	234	220	219	216
Width vulva	u	56*	56*	58*	66*	55*	58*	62*	85*	58*	63*	70*
Width anus	u	38*	na	56*	50	43+	36*	47	69*	na	35	50*
Tail	u	42*	52*	50*	52	54+	43*	50	55*	50	41	45*

X. diversicaudatum populations :-

A, USSR (Micoletzky, 1923)
B, USSR (Teploukhova, 1974)
C, Czechoslovakia (Erbenova, 1975)
D, England (Goodey et al., 1960)
E, Greece (Terlidou, 1967)
F, Italy (Martelli and Lamberti, 1967)
G, USA (Goodey et al., 1960)
H, West Germany (Martelli and Lamberti, 1967)
I, West Germany (Sturhan, 1963b)
J, Yugoslavia (Hrzic, 1978)
K, Poland (Szczygiel, 1974)

*, Values derived from published data.
+, Values derived from drawings of specimens in publications.
na, Not available.

TABLE 16 : Published means of morphometrics of male X. diversicaudatum from different populations.

		X. diversicaudatum									
		A	B	C	D	E	F	G	H	I	J
n		1	2	na	33	3	14	6	1	7	4
L	mm	4.3	4.19	4.33	4.9	4.5	4.06	4.2	4.7	4.24	4.46
a		81	78	70	76	79*	72	71	58	74	71
b		8.6	9.4	8.8	8.8	11*	8.6	8.7	8.8	8.5	8.6
c		93	97	87	78	102	92	76	89	87	82
c'		1.1	1.2*	0.85	1.1*	1.2+	1	1.2*	0.97	na	1.1
T	%	59	na	na	58	na	57	58	61	60	na
Odontostyle	u	134	130	132	143	136	128	128	131	137	139
Odontophore	u	75	na	79	83	65*	80	83	80	81	82
Spear	u	209	na	211	226	201*	212	211	212	217	221
Width great	u	53*	54*	62*	64*	57*	56*	59*	81*	57*	63*
Width anus	u	42*	36*	59*	50	43+	44*	45	55*	na	49*
Tail	u	46*	43*	50*	56	52+	44*	53	53*	48	54*
Spicula	u	69+	na	78	76	78+	79	72	82	na	76

X. diversicaudatum populations :-

A, USSR (Lectotype ; Pitcher et al., 1974)
B, USSR (Micoletzky, 1927)
C, Czechoslovakia (Erbenova, 1975)
D, England (Goodey et al., 1960)
E, Greece (Terlidou, 1967)
F, Italy (Martelli and Lamberti, 1967)
G, USA (Goodey et al., 1960)
H, West Germany (Martelli and Lamberti, 1967)
I, West Germany (Sturhan, 1963b)
J, Poland (Szczygiel, 1974)

*, Values derived from published data.
+, Values derived from drawings of specimens in publications.
na, Not available.

TABLE 17 : Percentage differences between largest and smallest values of published means of morphometrics of female and male X. diversicaudatum from different populations.

	Female	Male
	%	%
L	27	17
a	31	28
b	19	10
c	19	25
c'	38	19
V	19	-
T	-	7
Odontostyle	9	10
Odontophore	10	22
Spear	10	11
Width greatest	35	35
Width at anus	49	39
Tail	25	22
Spicula	-	16

CHAPTER VI

THE EFFECT OF OPERATOR AND MEASURING SYSTEM ERROR ON THE MORPHOMETRIC VARIABILITY OF A NEMATODE SPECIMEN

VI : 1 INTRODUCTION

Frederick and Tarjan (1978) examined the variability in measurements recorded from a single specimen of Pratylenchus coffeae and obtained by fourteen observers distributed in Europe and the USA who used the measuring systems available in their own laboratories.

A similar morphometrics exercise was completed during a European Science Foundation-financed Workshop on Taxonomy of Longidorid and Trichodorid Nematodes and Survey Techniques held at the Nematology Laboratory, Agricultural University, Wageningen, The Netherlands in 1979. Participants attending the workshop were asked to record a number of measurements from a single female specimen of Xiphinema incognitum.

A microscope measuring system, available in the Nematology Laboratory of the Agricultural University, was used by all participants in the exercise. Also, the measurements of the X. incognitum specimen were obtained by the same person on ten separate occasions and of a female specimen of X. diversicaudatum, at three temperatures 2 C, 20 C and 38 C, using the microscope measuring system available at the Nematology Section, Scottish Crop Research Institute (SCRI).

The results obtained were used to identify between operator,

within operator and rounding errors. Also the use of range, standard deviation and coefficient of variation percentage, when presenting morphometric data, were examined.

VI : 2 MATERIALS AND METHODS

The X. incognitum female was from a population extracted from soil associated with "bonsai" trees imported to Britain from Japan and was originally identified as X. americanum sensu lato. Lamberti and Bleve-Zacheo (1979) redescribed specimens from this population as X. incognitum. Specimens were heat killed, fixed in triethanolamine-formalin, processed to anhydrous glycerine by the rapid method of Seinhorst (1959) and mounted in anhydrous glycerine. The X. diversicaudatum female was extracted from soil from Fareham, England, heat killed, fixed in formalin-propionic acid 4:1 and processed as for X. incognitum.

A SM Lux Leitz microscope was used to examine the X. incognitum specimen in the Nematology Laboratory of the Agricultural University, Wageningen and a Reichart Diapan microscope was used at the SCRI. Both microscopes had drawing arms attached, and had 6.3 fold eyepieces, 2.5, 4, 10, 40 and 100 fold objectives.

Measurements recorded from the specimens were length of: body, body minus tail length, tail, odontostyle, odontophore, spear, anterior end to vulva and anterior end to the oesophageal and intestinal junction; also the body widths at the spear base, vulva and anus. Ratios calculated from the measurements were; a (length of body/body width at vulva), b (length of body/length of anterior end to the oesophageal and intestinal junction), c (length of body/length of tail), c' (length of tail/ body width at anus), V (length of anterior end to vulva x 100/length of body), V' (length of anterior end to vulva x 100/length of body minus length of tail) and S (length of

spear/body width at spear base).

The length of the body and length of the anterior end to the vulva were obtained by measuring a drawing, made of the specimen, with the aid of a length of copper wire at the Agricultural University, The Netherlands and a cartographers measuring wheel at the SCRI. All other measurements were obtained using an eyepiece graticule, previously calibrated for each objective using a micrometer slide.

All ratios were calculated at the SCRI from the measurements obtained by the participants. Small arithmetic differences are present in data in Tables 18, 19 and 20 due to the method of rounding the results to the nearest integer.

Measurements were recorded from the X. diversicaudatum specimen, at 2 C, 20 C and 38 C using a Reichart Diapan microscope, with drawing arm attached. The microscope and slide containing the X. diversicaudatum specimen were allowed to equilibrate in the hot and cold environments ("walk in" temperature controlled cabinets) overnight before being used. The measurements obtained at the low and high temperatures were recorded within one day for each temperature and separate days were used to record the measurements at each temperature. The measurements recorded at room temperature were each obtained on separate, non-consecutive, days at random times.

VI : 3 RESULTS

The mean, range, standard deviation (SD) and coefficient of variation percentage (CV) for each measurement and ratio obtained from the X. incognitum specimen by the ten participants are given in Table 18. The range, given for each measurement and ratio, indicates that variability was present and all data recorded by the participants. Expressing the difference in the range (largest minus smallest value) as a percentage of the mean value allows the measurements and ratios

to be ranked. The figures obtained for the range percentage of the mean, being independent of the unit of measurement, can be used for comparison between the structures measured. However, the range as a percentage of the mean uses only the smallest and largest observed values and does not include the other intermediate values. A coefficient can be obtained from standard statistical tables (Fisher and Yates, 1963) which permits the range value to be converted to a SD value. The SD derived from these tables is an approximation therefore the use of these tables is less satisfactory than calculating the true sample SD from all the recorded data.

Standard deviations were calculated for all measurements and ratios recorded. However SD cannot be used directly for a comparison of variability between the measurements and ratios recorded as it is dependent on the unit of measurement. Coefficients of variation (SD x 100/mean) give a precise indication of which data show the least and most relative variability. Ratio V and tail length had the smallest and largest CV values respectively (Tab. 18).

The measurements of one eyepiece graticule division, at the magnifications used to obtain the measurements recorded, are given in Table 18. Participants chose to use various magnifications except when measuring body length and length of the anterior end to the vulva when all used 63 fold magnification. Tail length and several other measurements were obtained when using either 252 fold or 630 fold magnification. The measurements of one eyepiece graticule division at 252 fold and 630 fold magnifications were 2.8 u and 1.1 u respectively. Therefore at 252 fold magnification a possible error of the unit of measurements of one eyepiece division, expressed as a percentage of the mean tail length value of 30 u, was 9.3% while at 630 fold magnification the same error was reduced to only 3.7 per

cent.

The specimen of X. incognitum that had been used for the previous exercise was measured on ten separate occasions by the same operator, each time using the same microscope measurements system. The mean, range, SD and CV percent obtained, for the same measurements and ratios used by the ten participants in the previous exercise, are given in Table 19. Data in Tables 18 and 19 allow three sources of measurement variability to be identified: between observer variability; within observer variability and rounding error variability caused when using the eyepiece graticule. Between observer variability was identified by comparing the variance (SD2) of measurements made by the one operator (Tab. 19) with that of measurements made by ten operators (Tab. 18) and assessing the significance using Variance Ratio tables (Fisher and Yates, 1963). No significant observer effects were detected for body length, body length minus tail length and ratios b, c', V, V' and S. However, all other measurements and ratios were significantly (P less than 0.05) more variable when the data were recorded by ten observers on one occasion than by only one observer on ten occasions.

When using the eyepiece graticule for measuring a structure one graticule division line (gdl) can be placed opposite one end of the structure. The opposite end of the structure will be opposite another gdl or, more probably, will lie somewhere between two gdl. Therefore the measurement error will be uniformly distributed between $\pm$ 0.5 of the measurement of one graticule division. The variability caused by rounding error when using the eyepiece graticule is therefore calculated as one twelfth of the measurement of one graticule division (Noble, 1964). A single rounding error was not calculated for body length minus tail length or the ratios as these each had at least two

rounding errors present. Rounding error in the remaining measurements contributed less than 10% to the SD values recorded except for body length and body width at the spear base where rounding error contributed one third and almost two thirds to the recorded SD values respectively.

Within-operator error variability was obtained by subtracting the rounding error from the SD2 values in Table 19. However, as rounding error contributes only a small variability, with occasional exceptions, the CV values presented in Table 19 can be used directly to evaluate the variability present in the data.

The results in Table 20 show the mean, range and CV percent values obtained from a single, female specimen of X. diversicaudatum, at 2 C, 20 C and 38 C, by one operator using the same microscope measuring system. No significant differences were present in the data recorded at the three temperatures.

VI : 4 DISCUSSION

Fourteen nematologists each measured the same structures in a single specimen of Pratylenchus coffeae using the microscope measuring systems available in their own laboratories. The average CV value, calculated for the measurements and ratios they used, was 4.5% (Frederick and Tarjan, 1978). In the exercise using X. incognitum, ten observers and a single measuring system the average CV value obtained, for the measurements and ratios used, was 8.8%.

Limited time and the use by the participants of an unfamiliar microscope measuring system probably contributed most to the larger mean CV value obtained in the X. incognitum exercise. It was not possible in either of these exercises to separate the variability attributable to operator error from the inherent error in the

measuring systems.

Frederick and Tarjan (1978) reported that CV values were considerably less when one observer, rather than when several observers, obtained the measurements. However, their two sets of CV values were obtained for nematode species of different genera and are therefore not strictly comparable. Nevertheless the trend reported by Frederick and Tarjan (1978) is supported by the analysis of data obtained in two exercises reported here (Tabs. 18 and 19). Therefore, a number of observations made by one observer each time using the same measuring system are likely to be less variable than those obtained by several observers when measuring the same nematode specimen.

Measurement variability in Frederick and Tarjan's exercises as in the exercises reported here may arise from several sources. Aberrations in the microscope system (Barron, 1965) e.g. field curvature, stage micrometer and eyepiece graticule accuracy etc.; rounding errors both when calibrating and when subsequently using the eyepiece graticule; mistakes in calculations and the influence of the observer when making the actual measurements can all individually contribute to the final recorded result. The sources of error can create a lack of precision and some may also be a source for bias in the final result. However, two sources of variability likely to contribute most to the final result, assuming the ideal microscope system is being employed and mistakes in calculations are minimised, are rounding errors when using the eyepiece graticule and the influence of the observer when recording the measurements. The use of new electronic measuring, recording and calculating devices used in conjunction with a microscope may reduce measurement variability (Boag, 1980).

The size range of a particular structure, particularly from a new nematode species, is less useful than the SD or CV as the range uses only the largest and smallest values obtained and so may be based on atypical extreme values. Therefore, the use of either of these values is advocated especially when the measurements of several paratypes of a new species are being presented. The CV values also allow the reliability of the measurements to be assessed.

Results from this, and Frederick and Tarjan's (1978) study suggest that when morphometrics of a nematode species reported by different authors are compared any differences in the morphometrics, in part, may be accounted for by operator and measuring system errors. Therefore, when comparing the morphometrics of different populations of X. diversicaudatum (Chapter V, Tabs. 15 and 16) apparent differences, in some instances, might be attributed to operator and, to a lesser extent, measuring system errors.

Operator and measuring system errors may not be the only extrinsic factors which affect the intrinsic variability of a nematode's morphometrics. Morphometrics of nematodes are most conveniently obtained from killed specimens and usually the killed nematodes are "fixed" in a suitable medium and processed to anhydrous glycerol in which they are subsequently mounted on microscope slides. It is possible therefore, that the method of killing, fixing or mounting a nematode may affect and alter the nematodes morphometrics.

TABLE 18 : Measurements and ratios obtained from one female specimen of X. incognitum by ten observers using the same microscope and measuring system.

Measurements and ratios		Mean (range)	SD	CV%	Magnification (X)	Graticule (one division)
Body	mm	1.79 (1.7-1.98)	0.087	4.9	63	-*
Body minus tail	mm	1.77 (1.67-1.95)	0.088	5	63/252** or 630	-*/2.8*** or 1.1
Tail	u	30 (25-44)	5.48	18.3	252 or 630****	2.8 or 1.1***
Odontostyle	u	89 (78-104)	6.54	7.3	"	"
Odontophore	u	52 (47-59)	3.83	7.3	"	"
Spear	u	142 (128-163)	9.2	6.5	"	"
Anterior to vulva	u	904 (850-990)	40.4	4.5	63	-*
Anterior to oesoph/intest junction	u	308 (241-366)	33.3	10.8	63 or 252****	-* or 2.8
Width at spear base	u	33 (29-43)	3.92	11.9	252 or 630****	2.2 or 1.1***
Width at vulva	u	44 (39-56)	4.77	10.8	"	"
Width at anus	u	27 (22-33)	2.84	10.4	"	"
a		41 (31-47)	4.45	10.8		
b		5.9 (5-7.5)	0.66	11.3		
c		61 (39-73)	10.2	16.7		
c'		1.1 (0.9-1.3)	0.11	10.5		
V	%	51 (49-53)	1.27	2.5		
V'	%	52 (50-55)	1.51	2.9		
S		4.3 (3.8-4.7)	0.27	6.3		

*, Eyepiece graticule not used.
**, Different magnifications used for measuring seperate structures.
***, Values refer to the different magnifications used.
****, Participants used different magnifications.

TABLE 19 : Measurements and ratios obtained from one female specimen of X. incognitum by one observer.

Measurements and ratios		Mean* (range)	SD	CV%	Magnification (X)	Graticule one division	Graticule round-off errors
Body	mm	1.77 (1.74-1.79)	0.03	1.5	63	0.052**	0.0043
Body minus tail	mm	1.74 (1.71-1.77)	0.03	1.5	63/ 397***	0.052**/ 1.8****	
Tail	u	27 (25-27)	0.63	2.4	397	1.8	0.15
Odontostyle	u	94 (92-97)	1.23	1.3	"	"	"
Odontophore	u	39 (38-40)	0.97	2.5	"	"	"
Spear	u	134 (132-135)	1.17	0.88	"	"	"
Antrior to vulva	u	863 (842-895)	27.4	3.2	63	52**	4.33
Anterior to oesoph/ intest junction	u	307 (300-313)	6.85	2.2	252	2.9	0.24
Width at spear base	u	31 (31-32)	0.42	1.4	397	1.8	0.15
Width at vulva	u	41 (41-43)	0.84	2	"	"	"
Width at anus	u	27 (25-29)	0.94	3.5	"	"	"
a		43 (40-44)	1.4	3.3			
b		5.8 (5.6-6)	0.16	2.8			
c		66 (64-72)	2.39	3.6			
c'		1 (0.9-1.1)	0.06	5.7			
V	%	49 (47-51)	1.71	3.5			
V'	%	50 (48-52)	1.71	3.5			
S		4.3 (4.2-4.4)	0.08	1.8			

*, n = 10.
**, Eyepiece graticule not used; figure represents one division on a cartographers measuring wheel, used to obtain the length of the structure.
***, Different magnifications used for measuring seperate structures.
****, Values refer to the different magnifications used.

TABLE 20 : Measurements and ratios obtained from one female specimen of X. diversicaudatum, at three temperatures, by one observer using the same microscope system.

Measurements and ratios		2 C Mean* (range)	CV%	20 C Mean* (range)	CV%	38 C Mean* (range)	CV%
Body	mm	3.9 (3.9-4)	1.3	3.92 (3.9-4)	1.5	3.93 (3.9-4)	1.6
Body minus tail	mm	3.86 (3.8-4)	1.3	3.88 (3.8-4)	1.5	3.89 (3.8-4)	1.6
Tail	u	41 (41-43)	2	42 (41-43)	2.4	42 (41-43)	2.5
Odontostyle	u	137 -	0	137 (137-139)	0.5	138 (137-139)	0.7
Odontophore	u	77 (77-79)	1.1	77 (77-79)	1.1	78 (77-79)	1.3
Spear	u	214 (214-216)	0.4	215 (214-216)	0.5	216 (214-218)	0.7
Anterior to vulva	mm	1.69 (1.63-1.75)	3.7	1.71 (1.63-1.75)	3.4	1.69 (1.63-1.75)	3.7
Anterior to oesoph/ intest junction	u	479 (472-483)	1.2	480 (472-483)	1.1	480 (472-483)	1.1
Width at spear base	u	44 (43-45)	2.4	44 (43-45)	2.3	45 (43-45)	1.9
Width at vulva	u	56 (56-58)	1.1	56 (56-58)	1.5	57 (56-58)	1.9
Width at anus	u	41 (41-43)	1.5	42 (41-43)	2.5	42 (41-43)	2.5
a		69 (69-71)	0.09	69 (69-71)	1.6	69 (67-71)	1.7
b		8.1 (8-8.3)	1.6	8.2 (8-8.5)	2.2	8.2 (8-8.3)	1.6
c		95 (93-95)	0.09	93 (90-98)	3.6	94 (90-98)	3.3
c'		1 (0.9-1)	5.6	1 (1-1.1)	4.7	1 (1-1.1)	5
V	%	43 (41-45)	4.2	44 (41-45)	3.5	43 (41-45)	3.9
V'	%	44 (41-46)	5.4	44 (41-46)	4.5	43 (41-46)	4.8
S		4.9 (4.9-5)	2	4.9 (4.8-5)	2.1	4.8 (4.8-5)	1.7

*, n = 10

CHAPTER VII

A COMPARISON OF THE EFFECTS OF SOME METHODS OF KILLING, FIXING AND MOUNTING ON THE MORPHOMETRICS OF XIPHINEMA DIVERSICAUDATUM.

VII : 1 INTRODUCTION

Morphometrical variability between populations of X. diversicaudatum, reported by several authors (Micoletzky, 1923, 1927; Goodey et al., 1960; Sturhan, 1963b and c; Martelli and Lamberti, 1967; Terlidou, 1967; Teploukhova, 1974; Erbenova, 1975; Hrzic, 1978), may be attributed to differences in biotopes. However, these authors used different methods of killing, fixing and mounting (= processing to glycerol) specimens.

The effects of different methods of preparing nematode specimens for taxonomic examination have been reported by several workers. The length of Ancylostoma caninum may be increased by up to 10%, depending on the fixative used (Scott, 1929); after fixation in glacial acetic acid the body lengths of Thynnascaris adunca increased by 20% compared with the length in live specimens (Soleim, 1976); a similar 25% increase in body length of Eustrongyloides tubifex was attributed to the effect of the fixative used (Fagerholm, 1979); Stone (1971) reported that the effects of processing Globodera rostochiensis larvae caused greater changes in body and stylet size than the difference between pathotypes; Curran and Hominick (1981) reported that qualitative characters, used in species diagnosis, and quantitative characters in adult male Romanomermis culicivorax and a Gastromermis

sp., could be altered using different methods of preparation. Maggenti and Viglierchio (1965) reported that much of the variation observed in fixed specimens of nematodes, particularly in qualitative characters, was caused by different methods of killing and fixation. Goodey (1959) reported that up to 20% shrinkage might occur in nematodes caused by the fixative and method of mounting used.

Few studies of the effects of preparation on members of the Longidoroidea have been reported. However, Lamberti and Sher (1969) compared the effects of different preparation techniques on L. africanus females and reported that significant increases (+26%) and decreases (-18%) occurred in several taxonomic ratios when compared with those obtained using a standard method. No similar study has been reported for the genus Xiphinema. Therefore, 28 combinations of killing and fixing and mounting were used to examine the effect of preparation techniques on the morphometrics and taxonomic ratios of X. diversicaudatum. The measurements and ratios obtained from the 28 treatments were also compared with those obtained from live specimens.

VII : 2 MATERIALS AND METHODS

X. diversicaudatum were extracted, using the method of McElroy et al. (1977), from soil collected from a mixed woodland at Inchmartine, Dundee. Suspensions of nematodes in water were collected from Baermann funnels after 15 hours, combined and thoroughly mixed. Ten female and five male specimens were hand-picked from each of 29 sub-samples and these specimens were used for the various treatments.

The four methods of killing, seven fixatives, three methods of mounting specimens in glycerol and the combinations of killing, fixing and processing used in the study are given in Table 21. Details of the methods are given in Hooper (1970) and are not repeated here. The

rapid glycerol-ethanol method of Seinhorst (1959) for processing nematodes to glycerol was used in the study. All nematode specimens were mounted in the appropriate fixative, glycerol or water on slides using a wax ring technique (De Grisse, 1969).

The 13 measurements and seven ratios, derived from the measurements obtained for each female X. diversicaudatum and used for the comparisons are given in Table 22. Also, the measurements and ratios obtained for each male nematode are given in Table 22. Measurements were obtained using a Reichart Diapan microscope, with drawing arm attached and with 6.3 fold eyepieces and 2.5, 4, 10, 40, 63 and 100 fold objectives. Structures measured on a millimetre scale and the spicula of males were measured from drawings made of each specimen.

The results were analysed statistically using the computing facilities available at the SCRI and at the Edinburgh Regional Computing Centre and the GENSTAT computer package (Alvey et al., 1982).

VII : 3 RESULTS

(See Table 22 for abbreviations of structures used in text).

Morphometrics of nematodes are most conveniently obtained from killed specimens. Therefore, although morphometrics were obtained from live specimens, the method chosen as standard for this study was to heat-kill specimens in water for 5 min at 60 C and then to make temporary water mounts of them.

An examination of the variance ratios calculated from the combined results for the female and male specimens showed that only the odontophore was not significantly affected by the different combinations of killing, fixing and mounting specimens. The spear and

odontostyle lengths had smaller coefficient of variation percentages (CV%) than the odontophore indicating that the spear and odontostyle were less variable than the odontophore. Therefore the treatment differences in the spear and odontostyle were significant but was not in the odontophore. The largest CV% values were 15.1% and 16.8% for the female anterior and posterior gonads respectively and 13.6% for the male testes (Tab.23).

The sex of the specimens did not significantly affect L, odontophore, anterior to anus nor the ratio S irrespective of the methods used but all other morphometrics, common to both sexes, were significantly affected by sex (Tab. 24). Few interactions between sex and treatment occurred and 11 morphometrics, common to both sexes, were not significantly affected. But width at anus, greatest width and ratio a were affected significantly by the methods used depending on the sex of the specimens. With females the width at anus differed significantly from the standard in one method and in 10 methods with males; greatest width was significantly affected by several methods with males but with females only those methods where the specimens were mounted in fixative significantly affected the measurements (Tab. 24).

Much varation was found in morphometric means from male and female X. diversicaudatum which had been prepared by the different methods used in the study (Tabs. 25 and 26). Significant differences were also recorded in the morphometric means of male and female specimens, prepared by different methods, when the morphometric values were compared with the mean values obtained for the standard method. Generally, the method of killing and the method of mounting the specimens in glycerol had similar affects. But, when the specimens were mounted only in fixative the mean body widths of the specimens

were significantly increased when compared with the standard method. The increase in mean body width was as much as 46% in males (H/FG/FG, greatest width) and 27% in females (FA4:1/FA4:1/FA4:1, width at spear base). The general effect of mounting specimens in glycerol seemed to be a reduction in size compared with the standard method. However, the anterior to oesoph-intest junction increased in size, often significantly.

Generally, the morphometrics of males were more often affected by the methods used than were the morphometrics of the female nematodes. L in males and females and L' in females were not significantly affected but L' in males was significantly affected by six of the methods used. The anterior to oesoph-intest junction in males and females were significantly affected by several of the methods and tail length was more frequently significantly affected in males than in females. With males the odontophore and spear were significantly affected each by three methods but with females the odontophore was only significantly affected by one method. With females the odontostyle and spear were significantly affected each by eight methods and in males the odontostyle was affected by only one method. Width at spear base in males was significantly affected by 26 of the 28 methods and by 15 methods with females. Greatest width in males and females was significantly affected by 14 and seven methods respectively and width at anus in males was significantly affected by 10 methods but in females only by one method. The ratios a, b, c, c' and S were significantly affected by several methods in males and females but males were more frequently affected than females; a, 22 and 12 (males and females respectively); b, 6 and 8; c, 22 and 3; c', 28 and 6 and S, 28 and 22 (Tabs. 27 and 28).

Live females differed from those treated by the standard method

in their anterior to oesoph-intest junction and width at spear base. These larger values caused the ratios b and S to differ significantly from those obtained using the standard method. In live males, only the morphometric means for L, spicula, odontostyle, odontophore, spear and ratio b were not significantly different from the means obtained with the standard method.

With female specimens the morphometrics recorded were least affected by the method H/FG/SG which affected only the odontostyle. Similarly, the methods H/FG/GE and H/H2O/GE each significantly affected only three of the morphometrics compared with the standard method. The method FA4:1 /FA4:1/FA4:1 most affected females, significantly affecting over half of the morphometrics (Tab. 29). In males four methods each caused five morphometrics to differ from those recorded using the standard method. However, the method H/TAF/GE significantly affected five morphometrics at P less than 0.05 and two at P less than 0.01 and one at P less than 0.001. Overall, this method appeared closest to the standard method having the least effect on the morphometrics of male X. diversicaudatum. The morphometrics of live male specimens differed more from those measured using the standard method than did those of any other treatment combination (Tab. 30).

VII : 4 DISCUSSION

Several workers have proposed methods for preparing nematodes which have been found satisfactory for morphometrical study or morphometrical examination of particular nematode species. However, none of the methods reported was satisfactory for all of the characters studied (Curran and Hominick, 1980; Lamberti and Sher, 1969; Maggenti and Viglierchio, 1965 ; Stone, 1971).

Only one population was used in the present study of the effects

of different methods of preparing X. diversicaudatum. Possible effects of these methods on other anatomical features of the specimens were not examined. However, other workers have also reported that the method of preparing nematodes can affect some of their anatomical detail (Curran and Hominick, 1980; Maggenti and Viglierchio, 1965).

The different methods had significant effects on the morphometrics; they differed both among themselves and from those of live nematodes. All of the methods examined altered significantly at least one morphometric mean compared with the standard method. Most methods affected several morphometric means and male specimens seemed to be more affected than female specimens.

Generally, methods of killing and methods of mounting the nematodes in glycerol each had similar effects on the specimens. However, the effects of the several fixatives examined seemed to be more variable. The fixatives usually caused significant swelling of the body diameters and shrinkage in lengths. When specimens were mounted in glycerol after fixation, body diameters shrank and became more similar to those recorded in the standard method. However, the anterior to oesoph-intest junction measurement became extended in fixatives and generally did not shrink when specimens were mounted in glycerol. Also, the width at spear base did not appear to become as reduced in size, as did other body diameters. No significant differences were found to occur in L with any of the methods examined. Therefore, it may be concluded that the elongation of the specimens caused by the increased length of the anterior to oesoph-intest junction was counteracted by a reduction in size of the remaining body length of the specimens.

Luc and Dalmasso (1975) presented an identification lattice of Xiphinema species; four of the twelve characters they used were the

morphometrics L, spear, ratio c' and V. During the present study L was not significantly affected by any of the methods used but spear, ratio c' and V were each significantly affected by several of the methods. Therefore, where two species are separated using morphometric differences in spear, ratio c' or V e.g. X. opistohysterum and X. pachtaicum; X. insigne and X. attorodorum; X. ensiculiferum and X. costaricense it should be ensured that the differences are not the result of different methods having been used to process the different specimens.

Probably at least some of the variability which exists between published morphometrics of X. diversicaudatum (see Chapter V:3) is attributable to different methods having been used to process the specimens. For example, Sturhan (1963b) measured heat-killed specimens in water whereas Martelli and Lamberti (1967) measured specimens which had been fixed in FAA and mounted by a rapid glycerol method. Unfortunately, however, few if any details of the methods used to process specimens are given by other authors. Therefore, it is not possible to apply correction factors, based on the results reported here, to the data in Tables 15 and 16 to compare the published morphometrics of X. diversicaudatum. Also, no correction factor to the published data could correct for possible effects of operator and measuring system error (see Chapter VI).

Other factors which might be considered are the possibility that some specimens were slightly flattened during the measuring process or that specimens continued to alter slightly for some considerable time after processing. The tail width of a X. diversicaudatum female reported by Martelli and Lamberti (1967) from West Germany was much greater than might be expected and this may have been caused by a flattening of the posterior part of the specimen. Professor J. Heyns

(pers. comm.) has observed the effect of such flattening in relation to type specimens of X. americanum reported by various authors. The flattening caused much morphometric variability and caused difficulties in accurate identification of specimens. However, Geraert (1961) reported a method for correcting measurements of nematode diameters which enables adjustments to be made in the event of any such error occurring.

Few studies on the effects of long-term storage of nematode specimens, after being processed in glycerol, have been reported. However, Esser (1974) reported that specimens of X. macrostylum which were re-examined and measured six years after originally being processed to glycerol were not significantly affected by storage. Many authors reporting morphometrics of X. diversicaudatum do not state how soon the nematodes were measured after processing the specimens to glycerol. Therefore, it is not known if any differences of this kind occurred. If differences did occur it is not known what, if any, correction factor may be necessary to compensate for different storage times.

From the results of this study it is evident that whenever morphometrics are used to identify Xiphinema specimens some allowance may have to be made if the method of processing the specimens differs from that of the type specimens. To identify correctly specimens to the specific rank, especially when morphometric criteria are being used, it may require that some specimens be processed using the method employed for the type specimens. However, this may not always be possible since many original descriptions of nematode species, including some in the genus Xiphinema, do not contain such details.

VII : 5 CONCLUSIONS

1) Different methods of killing, fixing and mounting nematodes in

glycerol can have significant effects on the morphometrics of specimens. Morphometrics from male specimens appeared to be more affected than those from females.

2) Morphometrics obtained from live and dead (killed in water at 60 C for 5 min) nematodes may differ significantly even when the killed nematodes are measured in water. Generally these differences appear to be caused by increases in size of the morphometrics of the dead nematodes.

3) Fixation of specimens, after killing, causes morphometric differences if compared with specimens prepared by a standard method (= heat killed in water at 60 C for 5 min). The fixatives caused significant swelling of the body diameters and shrinkage in length.

4) Mounting specimens in glycerol after fixation may result in a reduction of the effects caused by fixation. But, many morphometric differences remain after mounting specimens in glycerol, if compared with specimens prepared by a standard method.

5) Only the length of body of nematodes appears not to be affected significantly by killing, fixation or mounting specimens in glycerol. This appears to be the result of an extension of the anterior to oesophageal-intestinal length counteracting shrinkage occurring in the remaining body length.

6) It is not practical to recommend the adoption of a procedure for killing, fixing and mounting specimens in glycerol as all methods appear to affect at least one, if not several, morphometrics. However to identify correctly specimens to the specific rank, especially when morphometric criteria are being used, some specimens should preferably be processed using the methods employed for the type specimens.

TABLE 21 : Combinations of methods used to kill, fix and mount *X. diversicaudatum* specimens.

Method of killing	Fixative	Method of mounting	Abbreviations used in text
Heat killed in water (60 C for 5 min)	H2O	H2O	H/H2O/H2O (= SM)
	H2O	slow glycerol	H/H2O/SG
	H2O	glycerol-ethanol	H/H2O/GE
	TAF	TAF	H/TAF/TAF
	TAF	slow glycerol	H/TAF/SG
	TAF	glycerol-ethanol	H/TAF/GE
	FAA	FAA	H/FAA/FAA
	FAA	slow glycerol	H/FAA/SG
	FAA	glycerol-ethanol	H/FAA/GE
	FA4:1	FA4:1	H/FA4:1/FA4:1
	FA4:1	slow glycerol	H/FA4:1/SG
	FA4:1	glycerol-ethanol	H/FA4:1/GE
	FP4:1	FP4:1	H/FP4:1/FP4:1
	FP4:1	slow glycerol	H/FP4:1/SG
	FP4:1	glycerol-ethanol	H/FP4:1/GE
	FG	FG	H/FG/FG
	FG	slow glycerol	H/FG/SG
	FG	glycerol-ethanol	H/FG/GE
Hot FA4:1 (Seinhorst, 1966)	FA4:1	FA4:1	FA4:1/FA4:1/FA4:1
	FA4:1	slow glycerol	FA4:1/FA4:1/SG
	FA4:1	glycerol-ethanol	FA4:1/FA4:1/GE
Hot FP4:1 (Netscher and Seinhorst, 1969)	FP4:1	FP4:1	FP4:1/FP4:1/FP4:1
	4%F	4%F	FP4:1/4%F/4%F
	4%F	slow glycerol	FP4:1/4%F/SG
	4%F	glycerol-ethanol	FP4:1/4%F/GE
Vapour-phase using Formalin (Maggenti and Viglierchio, 1965)	FH2O 3:1	FH2O 3:1	Fv/FH2O 3:1/FH2O 3:1
	FH2O 3:1	slow glycerol	Fv/FH2O 3:1/SG
	FH2O 3:1	glycerol-ethanol	Fv/FH2O 3:1/GE
Live nematodes observed and measured in 0.7% water agar.			Live specimens

(= SM), Standard method.

TABLE 22 : Structures and ratios measured in X.diversicaudatum specimens prepared by different methods.

Structure		Abbreviation used in text
Length of body.	mm	L
Length of anterior end to the anus	mm	L'
Length of anterior end to the vulva*	mm	anterior to vulva
Length of anterior end to the oesophageal-intestinal junction	u	anterior to oesoph-intest junction
Length of body occupied by the antrior gonad*	u	anterior gonad
Length of body occupied by the posterior gonad*	u	posterior gonad
Length of tail	u	tail length
Length of odontostyle	u	odontostyle
Length of odontophore	u	odontophore
Length of odontostyle plus odontophore	u	spear
Body width at the spear base	u	width at spear base
Greatest body width	u	greatest width
Body width at the anus	u	width at anus
Spicula+	u	spicula
Length of body occupied by the testes+	mm	testes
L / greatest width		a
L / anterior to oesoph-intest junction		b
L / tail length		c
Tail length / width at anus		c'
Anterior to vulva x 100 / L*		V
Anterior to vulva x 100 / L'*		V'
Spear / width at spear base		S
Testes x 100 / L+		T

*, Female specimens only.
+, Male specimens only.

TABLE 23 : The effect of different killing, fixing and mounting techniques on some morphometrics recorded from female and male X. diversicaudatum.

FEMALES AND MALES		MEANS female	MEANS male	VARIANCE RATIO	SIGNIFICANCE+	CV%
Odontophore	u	80	80	1.150	NS	4.5
L	mm	4.74	4.71	1.803	**	7.2
Anterior to anus	mm	4.69	4.66	1.820	**	7.3
b		9.91	9.65	1.872	**	10.7
Odontostyle	u	129	127	2.030	**	3.7
Spear	u	209	207	2.058	**	2.9
Tail	u	46.7	49.5	2.240	***	9
c'		1.09	1.14	2.624	***	10.4
Anterior to oesoph/ intest junction	u	481	489	2.643	***	6.4
c		102	96	2.815	***	11
Width at anus	u	42.9	43.6	5.244	***	6.6
a		80	89	12.414	***	7.7
S		4.62	4.67	15.258	***	6
Width at spear base	u	45.5	44.6	16.340	***	6.7
Greatest width	u	59.3	53.3	17.877	***	7.5
FEMALES ONLY						
Anterior gonad	u	740		1.663	*	15.1
V	%	42.8		1.863	**	6.1
V'	%	43.1		1.872	**	6.1
Anterior to vulva	mm	2.03		1.919	**	8.3
Posterior gonad	u	793		2.144	**	16.8
MALES ONLY						
Spicula	u		63.3	1.608	*	9
Testes	mm		2.48	1.992	**	13.6
T	%		52.7	3.218	***	11.2

+, NS, not significant; *, P less than 0.05, **; P less than 0.01; ***, P less than 0.001.

TABLE 24 : The effect of the sex of the specimens and the interaction between sex and treatments on some morphometrics recorded from female and male X. diversicaudatum killed, fixed and mounted using several methods.

CHARACTER	EFFECT OF SEX		INTERACTION WITH TREATMENT	
	Variance ratio	Significance+	Variance ratio	Significance+
L	0.787	NS	1.005	NS
L'	0.939	NS	1.004	NS
Anterior to oesoph/ intest junction	6.365	*	1.215	NS
Tail	41.2	***	0.949	NS
Odontostyle	11.6	***	0.929	NS
Odontophore	0.032	NS	1.148	NS
Spear	7.811	**	0.957	NS
Width at spear base	7.446	**	1.495	NS
Greatest width	190	***	2.185	**
Width at anus	6.877	**	2.204	**
a	186	***	2.149	**
b	6.371	*	0.790	NS
c	32.3	***	0.933	NS
c'	16.1	***	1.246	NS
S	3.215	NS	1.940	NS

+, NS, not significant; *, P less than 0.05; **, P less than 0.01; ***, P less than 0.001.

TABLE 25 : Percentage differences in morphometric means of X. diversicaudatum females (n = 10) processed by different methods.

TREATMENTS*	L	L'	ANTERIOR		GONADS		TAIL	ODONTO-	
			o/i junc.	vulva	ant	post		style	phore
1 H/H2O/H2O (=SM)**	4.8	4.75	457	2.12	738	800	49	132	80
2 Live specimens	0.4	0.5	-11.1	4.2	-11	-7	-2.4	-2.2	0.5
3 H/TAF/TAF	2.3	2.4	5.7	-4.1	8.5	3.1	0.8	-1.2	0.2
4 H/FAA/FAA	-0.3	-0.3	9.2	4.6	8.5	14.1	-7.3	0.7	-0.9
5 H/FA4:1/FA4:1	-0.6	-0.6	5.7	-7.1	-5.1	0.8	-6.5	-2.3	-0.4
6 H/FP4:1/FP4:1	-1.8	-1.8	5.5	-3.4	6.8	0	-2.9	1.7	2.1
7 H/FG/FG	2.9	2.9	6.5	4	0	-9.4	-0.6	-0.8	-2
8 FA4:1/FA4:1/FA4:1	-3.1	-3.1	8.8	-8.8	-7.6	-8.6	-3.5	-2.3	-0.4
9 FP4:1/FP4:1/FP4:1	-4.6	-4.7	9.3	-5.3	-11.9	-8.6	1.8	-1.4	-3.1
10 FP4:1/4%F/4%F	-4.5	-4.6	6	-4.6	-1.7	-11	0.2	-1.9	-2.1
11 Fv/FH2O 3:1/FH2O 3:1	-3.6	-3.7	9.4	-6.1	3.4	4.7	1	0.2	-0.4
12 H/H2O/SG	0.7	0.8	1.6	-5	1.5	2.3	-10	-4.6	1.5
13 H/TAF/SG	-0.5	-0.4	5.4	-4.1	13	10.2	-14.9	-2.5	-3
14 H/FAA/SG	1.7	1.8	3.1	-2.5	3.4	3.1	-5.1	-4.1	-0.9
15 H/FA4:1/SG	-5.5	-5.4	5	-10.5	-5.9	-15.6	-8.6	-3.4	-2.1
16 H/FP4:1/SG	-4.9	-4.9	1.5	-10.3	-5.1	-13.3	-5.9	-0.8	1.5
17 H/FG/SG	-2	-2	6	-4	-3.4	-5.5	-7.1	-3.3	0.7
18 FA4:1/FA4:1/SG	-1.6	-1.6	7.8	-3.7	2.6	-3.1	-7.3	-2	-1.9
19 FP4:1/4%F/SG	-3.9	-3.9	5.5	-6.5	0.8	10.2	-4.9	-2.9	-1.1
20 Fv/FH2O 3:1/SG	-4.5	-4.5	3.5	-10.5	3.4	1.6	-5.9	-6.2	-0.4
21 H/H2O/GE	0.5	0.5	2.4	-4.8	0	2.3	-2.2	-1.1	-0.6
22 H/TAF/GE	1.1	1.2	6.4	0.2	10.2	12.5	-5.3	-5.2	-0.6
23 H/FAA/GE	0.7	0.8	4.2	0.4	7.6	8.6	-6.1	-2.1	-1.9
24 H/FA4:1/GE	-4.9	-4.9	2.2	-8.2	-4.2	-3.1	-6.1	-4.1	-4
25 H/FP4:1/GE	2.4	2.4	3.5	-4.1	2.5	-2.3	-4.3	-2.8	-2.2
26 H/FG/GE	-2	-1.9	-3.3	-7	-6.8	-4.7	-7.8	-2.4	-0.1
27 FA4:1/FA4:1/FA4:1	2.1	2.2	7	-1.2	2.5	-3.1	-7.3	-2.5	-0.6
28 FP4:1/4%F/GE	-3.4	-3.4	8	-6.8	2.5	3.9	-1.8	-4	-1.9
29 Fv/FH2O 3:1/GE	2.1	2.2	6.8	-0.5	1.7	-7.8	-2.4	-2.3	-0.6
LSD***									
P less than 5% ±	6.1	6.3	6.3	7	13.3	14.6	7.4	3	3.8
P less than 1% ±	8.1	8.3	8.3	9.2	17.5	19.1	9.7	4	5.1
P less than 0.1% ±	10.3	10.6	10.6	11.7	22.3	24.5	12.4	5.1	6.5

*, For explanation of abbreviations see Table 21.
**, Standard method.
***, Least significant differences as percentages of the standard method.

TABLE 25 : continued.

	SPEAR	BODY WIDTHS			RATIOS						
		s/ base	great	anus	a	b	c	c'	V	V'	S
1*	212	42	56	43	86	10.5	98	1.16	44	45	5
2	-1.2	9.2	0.9	2.8	-0.1	-9.5	2.7	-5.2	3.4	3.4	-9.5
3	-0.7	19.6	21	5.4	-15.7	-3.3	1.5	-4.7	-6.4	-6.6	-16.5
4	-0.8	16	18.4	3.5	-16.2	-8.6	8	-11.3	-4.4	-4.5	-14.1
5	-1.6	11.3	15	0.9	-13.9	-6	6.8	-8.1	-6.5	-6.6	-11.5
6	1.9	10.1	10.7	-1.4	-11.3	-7	1.7	-2.2	-1.6	-1.7	-7.4
7	-1.2	25.2	24.4	4.2	-17.4	-3.5	3.3	-5.1	-6.9	-6.9	-19.8
8	-1.3	27.1	26.7	11.7	-23.9	-11	0.1	-13.3	-6	-6	-21.2
9	-2.1	3.3	-0.2	-3.5	-4.7	-12.7	-6.6	5.3	-0.5	-0.4	-5.3
10	-2	5.2	-2.1	-0.9	-3.1	-10.1	-4.4	0.5	-0.2	-0.2	-6.8
11	0	6.8	6.2	0.9	-9.5	-11.8	-4.7	-0.3	-2.7	-2.7	-5.8
12	-2.3	5.7	2.3	-0.7	-2.2	-0.3	11.9	-10.2	-5.8	-5.9	-7.5
13	-2.7	0.5	2	-3.7	-2.8	-5.7	17.8	-12.2	-3.7	-3.8	-2.9
14	-2.9	5.2	2.5	0.5	-1.2	-1.3	7.5	-6.2	-4.3	-4.3	-7.5
15	-2.9	1.9	0.4	-3.3	-6.4	-9.8	3	-6.2	-5.3	-5.4	-4.7
16	0.1	7.3	5.3	1.6	-10.1	-6.3	1.1	-8	-5.8	-5.8	-6.7
17	-1.8	0.7	-2.3	-0.5	-0.1	-7.5	5.3	-7.3	-2.2	-2.2	-2.5
18	-1.9	8	3.6	-1.2	-5.4	-8.2	6.1	-7	-2.2	-2.3	-9.2
19	-2.2	7.5	3.4	-0.9	-7.9	-8.5	1.2	-4	-2.7	-2.7	-8.9
20	-4	2.4	4.6	-1.4	-9	-7.5	1.2	-5.3	-6.6	-6.6	-6.3
21	-0.9	5.2	-2.3	-2.1	2.3	-1.1	3.5	-0.9	-5.3	-5.4	-5.8
22	-3.5	-1.2	1.1	1.2	-0.5	-5	7.5	-7.1	-1	-1.1	-1.7
23	-2	7.8	3.7	2.3	-3.3	-3.4	8.1	-9.2	-0.1	-0.2	-9
24	-4.1	-0.7	1.1	-2.1	-6.5	-7	1.4	-4.8	-3.5	-3.5	-3.3
25	-2.6	3.1	4.1	0	-2.1	-1.2	6.9	-4.9	-6.4	-6.5	-5.5
26	-1.6	-4	-2.7	-4.7	0.2	9.3	6.5	-4.1	-4.9	-5	-2.5
27	-1.8	7.5	2.7	1.2	-1.2	-4.5	10	-9.2	-3.2	-3.3	-8.7
28	-3.2	8.3	3.9	1.2	-7.5	-10.3	-1.8	-3.6	-3.6	-3.6	-10.5
29	-1.2	11.1	11.4	0.2	-8.9	-3.7	7.3	-4.9	-2.5	-2.6	-11.1
LSD											
5%	2.5	6.7	6.5	6.1	6.6	8.8	9.8	8.7	5.2	5.2	4.8
1%	3.2	8.9	8.5	8	8.6	11.5	12.9	11.5	6.8	6.8	6.4
0.1%	4.1	11.3	10.9	10.2	11.1	14.7	16.4	14.7	8.7	8.7	8.1

*, for explanation of codes see previous page.

TABLE 26 : Percentage differences in morphometric means of X. diversicaudatum males (n = 5) processed by different methods.

TREATMENTS*	L	L'	ANT-o/i junc.	TES-TES	TAIL	SPICULA	ODONTO style	ODONTO phore
1 H/H2O/H2O**	4.64	4.58	458	2.71	55.2	65.2	126	82
2 Live specimens	7	7.3	9.6	-20.5	-17.8	-8.6	3.2	-3.2
3 H/TAF/TAF/	4.3	4.4	15.4	-10	-10.2	-8.6	3.3	0
4 H/FAA/FAA	0.8	1	5.1	-1.3	-10.5	6.1	0.5	-2.2
5 H/FA4:1/FA4:1	3.8	3.9	5.5	-5.6	-10.9	-7.7	1.4	-3.9
6 H/FP4:1/FP4:1	2.2	2.3	6	-23.6	-7.2	-2.8	1.7	-3.4
7 H/FG/FG	8.9	9.1	5.4	4.4	-4.4	2.4	0.6	-2.7
8 FA4:1/FA4:1/FA4:1	-0.8	-0.8	7.6	-4.7	-3.6	7.4	2.1	-3.9
9 FP4:1/FP4:1/FP4:1	-5.6	-5.6	4	-14.6	-10.2	-2.5	0	-5.1
10 FP4:1/4%F/4%F	-8.1	8.1	5.5	-12.8	-9.8	-4.9	1.7	-1.7
11 Fv/FH2O 3:1/FH2O 3:1	-3	-2.9	7.3	-12.8	-8.7	-5.2	5.6	-5.4
12 H/H2O/SG	0.2	0.4	5.8	-9.1	-17.4	1.2	1.1	-7.6
13 H/TAF/SG	1.5	1.7	6.9	-6.7	-11.2	-2.5	0.5	-5.6
14 H/FAA/SG	0.9	1	1.5	-2.7	-12.3	-3.7	-0.3	-6.6
15 H/FA4:1/SG	1.9	2	7	-13.1	-6.2	-4.9	0.2	-4.6
16 H/FP4:1/SG	-3.5	-3.4	-2	-19	-7.2	-8.3	-0.3	-2.2
17 H/FG/SG	3.2	3.4	9	-11.9	-9.1	-4.9	1.6	-3.2
18 FA4:1/FA4:1/SG	5.9	6.1	7	-4.1	-12.7	4.9	2.8	-1.5
19 FP4:1/4%F/SG	3.4	3.5	7	-3.7	-6.5	-2.5	0.2	-2.2
20 Fv/FH2O 3:1/SG	8.6	8.9	15	3.8	-14.1	4.6	1.4	-2.2
21 H/H2O/GE	-4.8	-4.8	0.9	6.5	-10.9	-3.7	1.1	-6.4
22 H/TAF/GE	3	3.1	6.9	-10.5	-10.2	-3.7	0	-2
23 H/FAA/GE	1.7	1.8	8	-15.6	-11.6	-4.9	-0.8	-1
24 H/FA4:1/GE	4	4.2	7.5	-18.2	-13.4	-7.4	0.2	-5.6
25 H/FP4:1/GE	1.9	2.1	10.6	-9.2	-13.8	-7.4	2.1	0
26 H/FG/GE	0.5	0.7	4	-11.7	-15.6	-12.3	-1.1	-2.4
27 FA4:1/FA4:1/GE	0	0.2	9	-5.2	-15.6	0	-0.2	-3.4
28 FA4:1/4%F/GE	2.2	2.3	7.6	3.7	-6.5	3.4	1	1
29 Fv/FH2O 3:1/GE	4.9	5.1	13.6	-15.6	-11.2	-7.4	0.3	-1.2
LSD***								
P less than 5% ±	9.7	5.4	7.3	15.7	10.4	11	5	5.7
P less than 1% ±	12.8	7.1	9.6	20.7	13.7	14.5	6.6	7.6
P less than 0.1% ±	16.5	9.2	12.4	26.6	17.7	18.8	8.5	9.8

*, For explanation of abbreviations see Table 21.
**, Standard method.
***, Least significant differences as percentages of the standard method.

TABLE 26 : continued.

	SPEAR	BODY WIDTHS s/ base	great	anus	a	b	c	c'	S	T
1*	208	38.6	47	40.6	99	10.1	84	1.36	5.4	58
2	0.7	19.2	19.6	8.6	-9.6	-1.9	30.8	-24.3	-15.6	-25.6
3	2	12.4	11.5	2.5	-6.7	-9.4	17.7	-12.5	-9.3	-13.5
4	-0.6	38.3	42.1	28.1	-29.1	-3.7	13.1	-29.5	-28.2	-2.2
5	-0.7	18.1	16.6	10.8	-20.8	-1.4	16.9	-19.1	-15.8	-9.1
6	-0.3	20.7	29.4	13.3	-20.3	-3.3	10.1	-18.4	-16.9	-25.2
7	-0.7	40.9	46.4	25.1	-25.6	3.6	13.9	-22.8	-29.4	-3.9
8	-0.3	39.9	41.3	22.7	-29.3	-7.5	3.1	-20.6	-28.3	-3.9
9	-2	13.5	11.1	3.4	-15.2	-9	6.4	-13.2	-13.5	-9
10	0.4	14.5	4.7	8.4	-12.4	-12.8	2.4	-16.2	-12.6	-5.1
11	1	12.4	4.2	3	-6.4	-9.3	6.4	-11	-9.8	-10.6
12	-2.3	14.5	3	3.9	-2.7	-5	22	-20.6	-14.8	-9.2
13	-1.9	8.8	3.8	2.5	-1.6	-4.4	14.6	-13.2	-10	-8.2
14	-2.8	10.4	7.6	5.4	-6.4	-0.3	15.9	-16.9	-12	-3.6
15	-1.7	13.5	12.3	1.5	-9.5	-4.4	9.5	-7.4	-13.5	-14.7
16	-1.1	13	10.2	6.9	-12.4	-1.2	4.2	-13.2	-12.6	-16.4
17	-0.3	9.8	3.4	-2	-0.5	-5	15.1	-10.3	-9.3	-14.6
18	1.2	18.6	14	6.4	-7.2	-0.3	22	-17.6	-14.8	-9.5
19	-0.8	18.6	14.9	6.9	-10.2	-2.7	11.5	-12.5	-16.5	-7
20	0	18.6	18.3	10.8	-7.2	-5.2	27	-22.1	-15.8	-4.5
21	-1.8	8.3	2.6	0.5	-7.4	-5.2	7.2	-11	-9.4	-12.1
22	-0.8	3.1	2.6	7.9	0.1	-3.4	15.4	-16.9	-3.9	-12.8
23	-0.9	10.9	13.6	6.9	-10.6	-5.6	15.6	-16.9	-10.6	-17.1
24	-2.1	9.8	12.3	4.4	-7.8	-3	20.9	-16.9	-10.1	-21.3
25	1.2	9.8	3.4	3.9	-1.8	-7.6	18.3	-16.9	-8	-10.9
26	-1.6	6.2	0.4	2	-0.2	-3	19.5	-16.9	-7.6	-12.1
27	-1.4	16.6	12.8	2	-11.6	-8.1	19.1	-16.9	-15.6	-4.8
28	1	15.5	11.9	6.9	-8.8	-4.7	10	-12.5	-12.6	1.9
29	-0.3	16.6	13.6	8.9	-7.6	-6.9	19.3	-18.4	-14.6	-19.2
LSD										
5%	2.1	8.1	12.3	7.9	4.7	7.6	9.5	6.2	3.7	12.7
1%	2.8	10.7	16.2	10.3	6.2	9.9	12.5	8.1	4.9	16.8
0.1%	3.5	13.8	20.9	13.3	8.1	12.8	16.2	10	6.3	21.6

*, For explanation of codes see previous page.

TABLE 27 : The significance and number of different methods of killing, fixing and mounting specimens, compared with a standard method, affecting some morphometrics of female X.diversicaudatum

Morphometrics.	Number of methods of killing, fixing and mounting specimens significantly different from the standard method.		
	P less than 5%	P less than 1%	P less than 0.1%
L	0	0	0
L'	0	0	0
Anterior gonad	0	0	0
Posterior gonad	1	0	0
Odontophore	1	0	0
V	10	1	0
V'	10	1	0
c'	6	2	0
b	8	2	0
Anterior to vulva	7	3	0
Spear	8	4	0
Width at anus	1	1	1
c	3	1	1
Tail	4	2	1
Anterior to oesoph/ intest junction	11	5	1
Odontostyle	8	6	2
Width at spear base	15	8	5
a	12	10	6
Greatest width	7	7	7
S	22	17	12

TABLE 28 : The significance and number of different methods of killing, fixing and mounting specimens, compared with a standard method, affecting some morphometrics of male X. diversicaudatum

Morphometrics	Number of methods of killing, fixing and processing specimens, significantly different from the standard method when :		
	P less than 5%	P less than 1%	P less than 0.1%
L	0	0	0
Spicula	1	0	0
Odontostyle	1	0	0
Odontophore	3	1	0
Spear	3	1	0
Testes	3	1	0
L'	6	4	0
b	6	1	1
T	10	5	2
Tail	13	6	2
Anterior to oesoph/intest junction	12	5	3
Width at anus	10	6	4
Width greatest	14	7	4
c	22	18	11
Width at spear base	26	20	14
a	22	22	15
c'	28	27	27
S	28	27	27

TABLE 29 : The significance and number of morphometric differences caused by different methods of killing, fixing and mounting female X. diversicaudatum when compared with a standard method.

Method of killing, fixing and mounting nematodes.	Number of morphometrics significantly different from the mean of the standard method when :		
	P less than 5%	P less than 1%	P less than 0.1%
H/H20/H20		(standard method)	
H/FG/SG	1	0	0
H/H20/GE	3	0	0
H/FG/GE	3	0	0
H/FP4:1/GE	4	0	0
FP4:1/4%F/4%F	2	1	0
H/FA4:1/SG	8	1	0
FP4:1/FP4:1/FP4:1	3	2	0
H/FAA/SG	3	2	0
Fv/FH20 3:1/ FH20 3:1	5	3	0
H/FP4:1/SG	6	3	0
H/H20/SG	7	3	0
FA4:1/FA4:1/SG	3	1	1
FP4:1/4%F/SG	3	1	1
H/FAA/GE	3	1	1
FA4:1/FA4:1/GE	5	1	1
H/TAF/GE	3	2	1
H/FA4:1/GE	3	2	1
FP4:1/4%F/GE	7	3	1
Fv/FH20 3:1/SG	7	4	1
Live specimens	4	3	2
H/TAF/SG	4	3	2
H/FP4:1/FP4:1	4	4	2
Fv/FH20 3:1/GE	5	4	2
H/TAF/TAF	6	6	4
H/FA4:1/FA4:1	7	4	4
H/FAA/FAA	6	5	4
H/FG/FG	7	6	4
FA4:1/FA4:1/FA4:1	11	7	5

TABLE 30 : The significance and number of morphometric differences caused by different methods of killing, fixing and mounting male X. diversicaudatum when compared with a standard method.

Method of killing, fixing and mounting specimens	Number of morphometrics significantly different from the mean of the standard method when :		
	P less than 5%	P less than 1%	P less than 0.1%
H/H20/H20		(standard method)	
H/TAF/GE	5	2	1
H/TAF/SG	5	3	2
H/FG/SG	6	3	2
H/H20/SG	6	3	2
H/FA4:1/SG	7	3	2
Fv/FH20 3:1/ FH20 3:1	7	4	2
H/FAA/SG	8	5	2
H/FG/GE	5	4	3
H/FP4:1/SG	5	4	3
FP4:1/FP4:1/FP4:1	6	4	3
H/FP4:1/GE	7	5	3
H/FA4:1/GE	11	5	3
H/FAA/GE	9	6	3
FP4:1/4%F/SG	6	4	4
FP4:1/4%F/GE	6	4	4
FA4:1/FA4:1/SG	8	5	4
H/H20/SG	7	6	5
FP4:1/4%F/4%F	7	6	5
H/TAF/TAF	8	6	5
FA4:1/FA4:1/GE	9	6	5
H/FA4:1/FA4:1	8	7	5
Fv/FH20 3:1/GE	10	7	5
Fv/FH20 3:1/SG	10	10	5
FA4:1/FA4:1/FA4:1	7	6	6
H/FAA/FAA	8	7	6
H/FG/FG	8	8	6
H/FP4:1/FP4:1	9	8	7
Live specimens	12	10	7

CHAPTER VIII

MORPHOMETRIC VARIABILITY BETWEEN POPULATIONS OF XIPHINEMA DIVERSICAUDATUM

VIII : 1 INTRODUCTION

Much variability is evident in the published data on the morphometrics of different populations of X. diversicaudatum (Chap. V:3). This variability in species morphometrics may be the result of operator error, measuring system error, different methods of killing, fixing and mounting the specimens (Chaps. VI and VII) or may be natural variation resulting from populations having adapted to survive in different biotopes.

Cultures of X. diversicaudatum from biotopes from different countries and continents were collected at the SCRI. Specimens from each culture were killed, fixed, mounted and measured using

standardised techniques to assess morphometric variability due to biotopic influence. The different cultures of X. diversicaudatum were maintained as breeding colonies using a standardised method. After four years, morphometrics from specimens from some of the cultures were compared with the morphometrics of the original specimens to assess the possible influence of a change in biotope on size and morphology of these populations.

VIII : 2 MATERIALS AND METHODS

VIII : 2:1 Populations of X. diversicaudatum

Cultures of X. diversicaudatum populations were collected in small quantities of soil c. 1 kg from 26 biotopes from 12 European countries; the United States of America and New Zealand (Tab. 31; Fig. 15). All of the cultures were from field populations except those from Dundee (glasshouse), Les Adrets, and Wageningen each of which were from glasshouse populations.

Upon receipt of each culture at the SCRI ten female and five male specimens were extracted using the method of McElroy et al.(1977) and these specimens were used for morphological and morphometrical studies. The remaining soil with nematodes was put into a series 30 cm diam. plastic pots each with a plant of Rubus idaeus cv. Malling Jewel, Fragaria x ananassa cv. Cambridge Favourite and Rosa sp. and maintained in a heated glasshouse (18 C) with natural daylight (Note: The soils containing X. diversicaudatum were placed in 30 cm diam. plastic pots as 2 to 5 cm layers of soil interspaced with 5 cm layers of washed, coarse sand. Water was added to the pots as infrequently as possible, and then only in amounts sufficient to prevent the host plants from wilting. This culturing method has been found to be satisfactory for producing large numbers of longidoroid nematodes under glasshouse conditions).

Ten female and five male specimens were extracted from each of seven populations, four years after the establishment of the populations at the SCRI. The morphometrics obtained from these specimens were compared with the morphometrics obtained from the original specimens from the seven cultures.

VIII : 2 : 2 Morphology and morphometrics

Ten female and five male specimens from each population of X. diversicaudatum were heat killed and fixed with triethanolamine/formalin (Courtney, Polley and Miller, 1955) using the method of Seinhorst (1966) and processed to glycerol using a slow replacement method.

A Reichart Diapan microscope, with drawing arm attached, and with 6.3 fold eyepieces, 2.5, 4, 10, 40, 63 and 100 fold objectives, was used to examine and obtain measurements of the specimens. The measurements and ratios obtained for each specimen are listed in Tab. 22 (Chap. VII).

VIII : 2 : 3 Analysis of data

The results obtained from the morphometric study of the 26 populations and from the subsequent morphometric study of seven of the populations were analysed statistically using the computing facilities at the SCRI and at the Edinburgh Regional Computing Centre. The morphometrics obtained from each population were analysed individually using the GENSTAT computer package (Alvey et al., 1982). Canonical variate analysis (CVA), was used to make an objective assessment of the relative similarity of populations, based on five selected morphometric features, L, V, c', odontostyle and odontophore lengths. Single-linkage cluster analysis, which formed part of the CVA program, was used to compile a dendrogram showing the clustering of populations

at different levels on a scale of similarity. The similarity values, S, between each pair of populations were calculated as $S=(1-D/10) \times 100\%$ where D was the Mahalanobis' distances calculated in the CVA.

VIII : 3 RESULTS

(See Table 22 for abbreviations of stuctures used in text)

VIII : 3 : 1 Morphometric differences between populations of X. diversicaudatum.

The populations of "X. diversicaudatum" received at the SCRI belonged to the group of Xiphinema species in which the females have two genital branches of similar length and structure and which contain a pseudo Z differentiation. Furthermore, most individuals had rounded, digitate tails and the apophyses present in the pseudo Z differentations in the female genital tracts were invariably globular, comprised of a central, spherical, refrigent portion surrounded by a less refrigent part, usually lobed. Males were relatively common in each population. the 26 populations of X. diversicaudatum examined constituted a homogeneous species with a more or less continuous pattern of morphometric variation (Tabs. 32 and 33). Some of the more important characteristics of the populations studied were:-

Pops. 1 and 2, Dundee, Scotland. Population 1 was the most northerly situated population of X. diversicaudatum in Britain and the biotope probably reflects the northern boundary for the survival of the species in the British Isles. Mean body length for females was larger and mean spear length was smaller for the Dundee specimens than the measurements given by Goodey et al. (1960) for their British specimens (5.2 vs 4.9 mm, mean body lengths; 215 vs 228 um, mean spear lengths). The morphometrics of specimens from pop. 2, which was originally from the field site of pop. 1, but which had been maintained for four years as a culture in a heated glasshouse, were significantly smaller than the morphometrics of specimens from pop.

1, (Tabs. 32 and 33).

Pops. 3 and 4, Cupar Kilsyth, Scotland. The specimens from pop. 3, were generally smaller than the specimens from pop. 4, and the mean body length for pop. 4 was most similar to that of pop. 9. Also, in most other respects pop. 4 was more similar to pop. 9 than to other, geographically more closely related populations.

Pops. 5, 6, 7, 8, 9 and 10, various locations throughout England. Much morphometric variation was apparent between these populations. Pop. 5 had mean values for odontostyle, odontophore, spear and tail lengths most similar to pop. 26 from Poland. These values were the largest recorded for these structures during the study. Therefore, pop. 5 was quite unlike any of the other populations from Britain due to its large morphometric means for the aforementioned structures. The British populations described by Goodey et al. (1960) were from Kent and Somerset in southeast and southwest England respectively. Pops. 8 and 10 were from southeast and southwest England respectively. However, pops. 8 and 10 and pops. 5, 6, 7 and 9 all had smaller morphometric means for L, odontostyle, odontophore, spear and tail than the values given by ibid.

Pops. 11 and 12, Wrekin and Nevern, Wales. Pop. 12 generally had larger morphometric means than pop. 11. Also, these populations in common with all the other British populations had smaller morphometric means for odontostyle, odontophore, spear and tail length than the values given by ibid for their British specimens.

Pops. 13 and 24, Saint-Katherina-Lombeek, Belgium and Holzieken, Switzerland. The morphometrics of specimens from these two populations were similar (Tabs. 32 and 33) and they, together with pops. 10 and 11 constituted a sub-group of populations (Figs. 16, 17, 18 and 19).

Pop. 14, Kostinbrod, Bulgaria. This population could be placed in a group comprising pops. 15, 18, 19 and 23 in which the morphometric means for L and spear length were less than 4.5 mm and less than 200 um respectively. Pops. 14 and 19 had the smallest mean length for odontostyle (120 um) recorded in the study.

Pop. 15, Les Adrets, France. X. diversicaudatum is found in field soils in the Camargue and around Montpellier in southern France. To the east of Montpellier, X. diversicaudatum was found only in soils in glasshouses and not in the field. Therefore, pop. 15 was probably introduced to Les Adrets and its origins are unknown. The mean value for ratio c' for pops. 14, 15 and 20 was 1.3, the largest value recorded in the present study for this ratio.

Pops. 16, 17 and 18, Liguria, Lombardi and Piemonte in northern Italy. Similar morphometric means were recorded for all three populations. The mean L value for pops. 16 and 18 was 4.1 mm which was the lowest mean L value recorded in the study. Generally, the morphometrics from these three populations were similar to the morphometrics of an Italian population (Martelli and Lamberti, 1967). However, the mean values for odontostyle, odontophore and spear lengths of pops. 16, 17 and 18 were somewhat smaller than the mean values given by ibid. for these structures.

Pop. 19, Wageningen, The Netherlands. As with pop. 15, this population was obtained from soil from a heated glasshouse and its origin is unknown although it is believed to be from field soil in the locality (J. W. Seinhorst, pers. comm.). This population had the smallest mean values for odontostyle and spear lengths recorded during the study (120 um and 195 um).

Pop. 20, Alexandra, New Zealand. X. diversicaudatum appears to have an exclusively European natural distribution but is also present in New Zealand and the USA. Therefore, pop. 20 represents the most

geographically distant population from the species natural distribution area. However, apart from a somewhat large mean c' value, similar to pops. 14 and 15, pop. 20 is generally morphometrically similar to many of the other populations studied and was most similar in L, odontostyle, odontophore, spear and tail lengths to pop. 2.

Pops. 21 and 22. Sandefjord and Rygge, Norway. These were obtained from the most northern biotopes in Europe at which X. diversicaudatum exists. The two populations were morphometrically similar to each other and pop. 21 had the smallest mean value for V, 40%, recorded, similar to pop. 25.

Pop. 23, Cazalegas, Spain. This populations was obtained from the most westerly biotope examined in the study. The nematodes, although similar to specimens from other populations, had the smallest mean values recorded in the study for odontophore length (72 um) and for tail length (42 um) and the largest mean values for ratios a (97) and c (117). Pop. 23 could be distinguished from other populations of X. diversicaudatum examined in the study by its having small mean values for odontostyle (124 um), odontophore (72 um), spear (196 um) and tail length (42 um) and a relatively large mean value for body length (5.00 mm).

Pop. 25, San Diego, USA. This population is probably a representative of the species surviving outwith its natural European distribution, similar to pop. 20. The morphometric means recorded for this population were similar to those for several other European populations of X. diversicaudatum and were most similar to those recorded for pop. 6. Morphometric means given for specimens of X. diversicaudatum from the USA by Goodey et al. (1960) differ from the mean values recorded from specimens examined in the present study. For example, the mean values given by ibid. are smaller than the

values obtained in the present study for L (4.2 vs 4.6 mm), a (68 vs 83), c (90 vs 96) and c' (1.1 vs 1.2). Conversely, larger values were given by ibid. for lengths of odontostyle (131 vs 126 um), odontophore (86 vs 79 um), spear (217 vs um), tail (50 vs 48 um) and ratio V (45 vs 40%).

Pop. 26, Nowy Sacz, Poland. This population had the largest mean length for odontostyle (154 um), spear (241 um) and tail (56 um) recorded in the study and was most similar to pop. 5. The morphometric means given by Szczygiel (1974) for specimens of X. diversicaudatum from Poland were all smaller than the values recorded for pop. 26 in the present study.

As all the populations studied were deemed to belong to X. diversicaudatum the grand mean for each morphometric was compared with the morphometric means obtained for each population. For structures measured in both males and females the grand means were similar for both sexes. The percentage differences between the morphometric means, obtained from groups of 10 females and five males from the different populations studied, and the grand means for the morphometric characters studied are given in Tabs. 32 and 33. For all but one of the morphometric characters studied at least one of the populations was statistically significantly different from the grand mean. An exception was T in the males for which no significant differences occurred between the population means and the grand mean.

With females the differences between the smallest and largest morphometric means, expressed as a percentage of the grand means ranged from 10% for V to 57% for posterior gonad. Similarly, for males the percentage differences ranged from 21% for S to 63% for greatest width. Odontostyle, odontophore, spear, tail and L had averages of 26% and 30% differences between the smallest and largest

morphometric means for females and males respectively.

The percent coefficient of variation (CV), obtained for the different morphometric structures, measures variation within the populations studied. It was found to be similar for male and female specimens. Spear, odontostyle, odontophore and S CV's were the smallest values obtained and c, c' and the length of body occupied by the male and female genital tracts had the largest CV values recorded (Tabs. 32 and 33).

With females, populations 2 and 11 had morphometric means most similar to the grand means, each having only two values significantly different from the corresponding grand means. Populations 5, 23 and 26 had most means significantly different from the grand means. Also, males in populations 5 and 23 had most significantly different mean values when compared with the grand mean values but population 3 had no significant differences between its morphometric means and those of the grand means (Tabs. 34 and 35).

VIII : 3 : 2 Morphometric similarity between populations of X. diversicaudatum.

Five morphometric characters, L, V, c', odontostyle and odontophore were chosen because they had been used by Luc and Southey (1980) and thus a compairson could be made with their results. Fig. 16 shows the two-dimensional placings of the 26 populations studied relative to the first two axes of the CVA based on population female means for the five variates. Figs. 17 and 18 show similar plots for axis 1 and 3 and 2 and 3 respectively. Although five axes were available for plotting 78.4% of the variance was accounted for by axis 1 and 2 and 91.8% by axis 1, 2 and 3. Thus, as almost 92% of the potential for separating populations were present in the first three axes the final two axes were not plotted.

Some populations from the same geographic areas e.g. pops. 21 and 22; 15, 16, 17 and 18, were found to cluster together i.e. form morpho-groups, which suggests that only a small amount of geographic differentiation exists between them. However, these trends are not conspicuous and all the populations tend to form a homogenous group with only an occasional population outlier e.g. populations 5 and 26 and 23. Tab. 36 gives "importance values" for each of the five characters used for the analysis; the values were calculated by multiplying the appropriate loading used in the analysis by the standard deviation of the population female means for each character. Odontostyle and odontophore lengths contributed most to the separation of populations on axis 1, L and odontophore lengths on axis 2 and c' and odontostyle length on axis 3.

The results of a single-linkage cluster analysis are presented in Figs. 16, 17 and 18 and as a dendrogram (Fig. 19). Ten populations clustered to form four groups at the 95% level of similarity; 20 populations formed three groups at 92.5%; pops. 1, 6 and 18 clustered with these other populations to form groups at 90%; all of these populations formed a single group and were joined by pop. 23, as a separate outlier, at 82.5%; pops. 5 and 26 formed a group at 87.5% but these populations did not cluster with the others until 80%. Therefore, all of the populations examined in the study formed a single homogeneous group at the 80% level of similarity (Figs. 16, 17, 18 and 19).

VIII : 3 : 3 Effect of biotope on the morphometrics of populations of X.diversicaudatum.

Most morphometric means obtained for population 1 were significantly larger than the values obtained for population 2. Exceptions were anterior to oesoph-intest junction, tail, odontophore,

V and S for females and tail, S and T for males and these values were not significantly different between the two populations. Populations 1 and 2, used in the present study, were obtained from the same biotope. However, population 2 was collected four years before population 1 and was kept as a culture in a heated glasshouse. Specimens used for the morphometric study were collected, on the same day, from the glasshouse population and from the natural field population. Because of the significant differences which occurred in the morphometric means between these two populations, specimens were collected from seven other populations which had also been maintained for four years in the glasshouse.

The morphometric means obtained from the specimens from the glasshouse populations were compared with the values obtained from the specimens taken from the original field populations (Tabs. 37 and 38). The mean L value for females was significantly larger for pop. 14-glasshouse than pop. 14-field. Similarly the mean L for females for pop. 17-glasshouse and pop. 24-glasshouse were significantly smaller than the mean L values obtained for the corresponding field populations. However, although the mean L values for males in pop. 14 showed the same significant trend as the mean L values for females in pop. 14 the mean L values for males in pop. 17-glasshouse and 24-glasshouse were significantly larger than the mean L values for pop. 17-field and pop. 24-field. This result, for the males in pop. 17, conflicts with the result obtained with the females in pop. 17. Also, the mean L value for males in pop. 20-glasshouse was significantly smaller than the mean L value for pop. 20-field. The mean anterior to vulva values obtained for the field and glasshouse cultures of the seven populations were not significantly different within each population. However, the values for testes (Tab. 22) were significantly larger in the glasshouse cultures of pops. 14, 17

and 24 and significantly smaller in the glasshouse culture of pop. 15 when compared with the values obtained for the corresponding field cultures.

Generally the mean values for anterior to oesoph-intest junction were not significantly different for each sex within each population. However, exceptions were the mean values obtained with males from glasshouse cultures of pop. 14 and pop. 24 which were significantly larger and smaller, respectively, when compared with the values obtained with the corresponding field cultures. The mean values for greatest body width, body width at anus, odontostyle and odontophore were significantly different for one and/or the other sex, within each population. The glasshouse cultures of each population consistently had larger mean values for these four values. However, mean values for body width at anus for males and females from pops.14 and 15 only were not significantly different between the glasshouse and field cultures of each population.

VIII : 4 DISCUSSION

Much variability is apparent in published morphometrics between populations of X. diversicaudatum (Chap. V:3). The results obtained in the present study suggest that some of the variability reported by the various authors, may be the result of differences existing between populations of X. diversicaudatum. Therefore, the reported variability may not be entirely the results of fixation artifacts or measurement error (Chaps. VI and VII).

The morphometric variability between populations of X. diversicaudatum in the present study was found to be somewhat larger than had previously been reported. For example, the percentage differences between the largest and smallest mean values for tail and spear lengths in the present study were 23% and 19% respectively but

in published morphometrics of X. diversicaudatum the values were only 18% and 19% ,respectively, (Chap. V, Tab. 17).

Techniques similar to those used to examine the taxonomic status of X. insigne and X. elongatum by Luc and Southey (1980) were used to establish morpho-groups of X. diversicaudatum populations. Luc and Southey (1980) reported that species of X. insigne, X. elongatum and X. savanicola clustered (i.e. formed a morpho-group) at the 75% level of similarity. Also, they reported that populations of X. insigne and X. elongatum formed into clusters at the 80% and higher levels of similarity. In the present study populations of X. diversicaudatum clustered at 95, 92.5, 90 and 87.5% levels of similarity and the morphometrically most different population, pop. 23, from the other populations clustered at the 82.5% level.

Specimens from each population used in the present study appeared to be anatomically similar and differed only in their morphometrics. Therefore, it was concluded that all of the populations belonged to the one species, X. diversicaudatum. The morpho-groups of populations established in the present study were therefore considered to be intraspecific groups of X. diversicaudatum.

The geographical origin of each population did not in general appear to influence the arrangement of populations into their morpho-group. However, two populations from Norway were grouped together but three populations from Italy were grouped together with populations from England and the USA. The morpho-groups of populations of X. diversicaudatum, therefore, appeared to be somewhat arbitary and clustered in a similar way to populations of X. insigne and X. elongatum (ibid) i.e. they did not always cluster according to their geographical origin.

The populations did not appear to form any morphometric clines. Populations with generally small morphometric means were recorded from biotopes in realtively close proximity to biotopes with populations with generally large morphometric means. For example, a population from Aylesford, England was morphometrically similar to populations from Italy and France which all had generally small morphometric means. But, a population from High Halstow, England, which is situated about 15 km north-east of Aylesford was morphometrically similar to a population from Kilsyth, Scotland and these populations generally had relatively large morphometric means somewhat similar to other British populations. It is interesting to speculate that the Aylesford population of X. diversicaudatum may be an introduction as is believed to be the case with X. pachtaicum ; the latter having been identified from nearby orchard soils (Taylor and Brown, 1976).

The results suggest that geographical location per se is not likely to be the only factor which determines the final morphometrics of a population of X. diversicaudatum. This is demonstrated by the morphometric changes which occurred when specimens from the Dundee (field) population were cultured in a glasshouse. After four years the morphometrics of the population in the glasshouse were significantly smaller than those obtained from the field population. Therefore, it is concluded that biotopic changes e.g. changes in geographical location, plant, host, soil type, climate etc. can affect significantly the morphometrics of X. diversicaudatum.

Variability apparent in published morphometrics of populations of X. diversicaudatum (Chap. V:3) therefore may not only result from fixation artifacts, operator and measuring system error but also from differences between the biotopes from which the specimens were collected.

Plant nematology relies on the "morpho-species" concept in taxonomy and morphometrics are used as a convenient way of mathematically describing specific structures. Where the morphometric (hence morphological) differences between populations are large and distinct the morphometrically most different populations may be proposed as new "morpho-species". Many morphometrics used in the taxonomy of the Longidoroidea were altered significantly in specimens of X. diversicaudatum prepared by different methods for examination by optical microscopy (Chap. VII). The largest and smallest means of several morphometrics and means obtained from a standard method from that study are given in stylised form in Figures 20 and 21. Also, the largest, smallest and grand means of morphometrics obtained from different populations of X. diversicaudatum are given in Figures 20 and 21. In the study examining preparation methods the ranges of values frequently overlapped between the treatments with the largest and smallest morphometric means. But, in the study examining the morphometrics of populations of the nematode the ranges of values in the populations with the largest and smallest morphometric means for a particular structure often were discontinuous between the two populations. These discontinuities in the ranges of morphometrics between populations of X. diversicaudatum could be used to refer groups of populations to separate specific rank. However, X. diversicaudatum in which males are common, is an amphimictic species unlike many other species in the Longidoroidea which are thelytokous. It is possible therefore to apply the objective biological species concept to this species rather than to rely on the subjective morphological species concept.

VIII : 5 CONCLUSIONS

1) Much variability is present in the morphometrics of X. diversicaudatum which results in significant differences occurring between populations.

2) The variability in the morphometrics of X. diversicaudatum is greater than has previously been reported and than that caused by employing different methods to process specimens for examination by optical microscopy.

3) Groups of populations of X. diversicaudatum with generally similar morphometrics (= morpho-groups) may be established using canonical variate analysis but all populations formed a homogenous group at the 80% level of similarity. In an independent study of three thelytokous species of Xiphinema, populations of all three species formed a homogeneous group at the 70% level of similarity. Therefore, similar studies in the future may use these results for comparison and, where nematode populations form homogeneous groups at the 80% or higher levels of similarity, these populations may be considered to comprise one species.

4) Geographical origin of the populations of X. diversicaudatum did not determine the composition of the morpho-groups and morphometric clines were not apparent. This suggests that the morphometrics of X. diversicaudatum are not primarily determined by the geographical locations of the populations.

5) Morphometrics of populations of X. diversicaudatum may be altered significantly by changing the nematodes biotopes e.g. changes in soil type, host plant, temperature, etc. However, components of the biotope interact with one another to form the biotope. Therefore a particular component of a biotope may be correlated with changes in

the nematodes morphometrics but, that component may not necessarily be related to these changes.

6) X. diversicaudatum shows much variability in its morphometrics and this variability probably reflects its ability to adapt to different biotopes. Thus the species poses a threat to those areas where it is not yet present.

TABLE 31 : Populations of X. diversicaudatum collected and kept at the SCRI.

Country	Location	Host Plant	Population number
Scotland	Dundee (field)	Sambucus nigra	1
Scotland	Dundee (glasshouse)	Rosa sp.	2
Scotland	Cupar	Fragaria x ananassa	3
Scotland	Kilsyth	Deciduous woodland	4
England	Ilkely	Lolium perenne	5
England	Bury St. Edmunds	Deciduous woodland	6
England	Harpenden	Lolium perenne	7
England	Aylesford	Scrubland	8
England	High Halstow	Deciduous woodland	9
England	Treswithian	Lolium perenne	10
Wales	Wrekin	Lolium perenne	11
Wales	Nevern	Rosa sp.	12
Belgium	Saint-Katherina-Lombeek	Fragaria x ananassa	13
Bulgaria	Kostinbrod	Ribes nigrum	14
France	Les Adrets	Rosa sp.	15
Italy	Liguria region	Vitis vinifera	16
Italy	Lombardi region	Rubus idaeus	17
Italy	Piemonte region	Prunus persica	18
Netherlands	Wageningen	Rosa sp.	19
New Zealand	Alexandra	Prunus armeniaca	20
Norway	Sandefjord	Senga sengana	21
Norway	Rygge	Senga sengana	22
Spain	Cazalegas	Vitis vinifera	23
Switzerland	Holzieken	Triticum spelta	24
USA	San Diego	Prunus persica	25
Poland	Nowy Sacz	Fragaria x ananassa	26

TABLE 32 : Percentage differences in morphometric means of X. diversicaudatum females (n = 10) from different populations.

POPULATIONS*	L	ANTERIOR		GONADS		TAIL	ODONTO-		SPEAR
		o/i junc	vulva	ant	post		style	phore	
Grand Means	4.68	504	1.98	767	819	48.5	131.7	79.6	211.3
1	11.6	0.1	16.3	17.3	14.5	-2	3.4	-0.7	1.9
2	-1.7	2	1.3	1	-3.8	5	-0.6	-2.3	-2.3
3	5.7	-0.1	2.3	9.1	5.4	-8.6	0.4	1.6	0.9
4	11.3	5.8	11.9	18.9	28.3	2.5	3.4	8.6	5.4
5	6.3	14.8	10	1.8	-2.3	15.5	13.9	12.6	-13.5
6	-2.3	-1.9	-4.6	1	-6.9	-8.6	-3.4	-3.2	-3.3
7	-4.6	2.6	-5.2	4.3	9.9	2.1	1.2	4	2.2
8	-11.2	3.3	-12.2	-5.5	-13	-6.4	-2	-0.4	-1.4
9	11.4	8.1	9.9	5.9	13	2.1	4.6	7.2	5.6
10	2.5	4.7	4.9	15.7	8.4	0.7	1.9	0	1.2
11	3.4	4.7	2.2	5.9	-0.7	-2.2	1.7	3.5	2.4
12	7.6	6.3	13	-0.7	6.9	6.6	4.9	6.6	5.5
13	8.7	3.8	7.4	5.9	-2.3	5	4.1	4.4	4.2
14	-8.2	-7.3	-5.9	-23.4	-14.5	9.7	-8.5	-5.9	-7.6
15	-8.1	-9	-7	-15.3	-6.9	5	-5.7	-5.8	-5.7
16	-12.4	-9	-11.8	-7.1	-3.8	-11.7	-3.6	-4.8	-4.1
17	-9.5	-6.9	-7.7	-2.3	-3.8	-8	-4.8	-6.6	-5.5
18	-11.6	-9	-12.8	-0.6	-16	-10.3	-6.6	-4.2	-5.7
19	-9.2	-7.8	-10.3	-15.3	-2.7	1.3	-8.5	-5.7	-7.5
20	-3.3	-0.3	-1.4	5.9	-6.9	1.7	-1.6	-2.2	-1.8
21	0.4	-3.4	-4	12.4	6.9	-0.6	-1.8	-2.4	-2
22	-3.9	-1.9	-7.8	9.1	20.6	-2	-2.8	-4.4	-3.4
23	6	-7.6	-10.5	-32.2	-28.2	-12.5	-5.9	-10.1	-7.5
24	6	2.9	4.8	1	9.9	1.3	3.4	4.4	2.8
25	-2.2	-7.8	-7.1	-8.8	-3.8	-0.1	-4.4	-1	-3.2
26	2.7	12.9	3.4	-3.1	-8.2	15.3	17.2	-9.5	14.3
LSD**									
P 5% ±	6.5	4.4	6.9	12.5	13.2	7.1	3	3.7	2
P 1% ±	8.6	5.8	9.1	16.4	17.3	9.4	3.9	4.9	2.7
P 0.1% ±	11	7.4	11.7	21	22.2	12	5	6.3	3.4
CV%***	7.4	5	7.9	14.2	14.9	8.1	3.4	4.2	2.8

*, For explanation of codes see Table 31.
**, Least significant differences as percentages of the Grand Means.
***, Coefficient of variation percentages.

TABLE 32 : continued.

POPULATIONS*	BODY WIDTHS			RATIOS					
	s/ base	great	anus	a	b	c	c'	S	V
Grand Means	45.8	59.6	44.1	79	9.3	97.3	1.11	4.63	42.3
1	2.6	4	6.1	6.9	11.8	13.2	-8.1	-1	4.1
2	-1.9	-4	-2.5	1.9	-3.9	-6.4	7.5	0.5	3.1
3	4.8	3.2	3.4	2	6.2	15.5	-11.9	-4	-3.3
4	5.3	5.2	10.4	7	6.5	9.6	-7.7	-0.2	-1
5	27.8	33.6	32.4	-20.5	-0.5	-7.8	-12.9	-10.8	3.5
6	0.5	0.7	-2.4	-3.4	-7.3	6.6	-11.2	-4.1	-2.1
7	-0.2	0.2	-4.1	-5.3	-7.3	-7.2	5.9	2.2	-0.6
8	-1.3	-1.8	5.2	-9.8	-14.1	-5.6	-11.3	-0.3	-1.1
9	2.4	6.4	6.1	6	4.8	10.8	-4.2	2.8	-3.2
10	4.4	3.2	2.9	-1.2	-2.3	2.2	-2.7	-3.3	2.1
11	0.9	2.4	-1.7	0.6	-1.3	5.2	-1.2	1.2	-1
12	1.1	1.7	2.2	5.3	0.9	0.5	3.9	-4.3	5.2
13	-1.3	2.9	0.9	5	4.5	3	3.4	5.4	-0.9
14	-5.2	-6.9	-6.8	-1.8	-1.2	-16.4	16.9	-2.8	2.2
15	-8.1	-9.2	-12.5	0.6	0.8	-13	19.3	2.2	1.3
16	-8.1	-8.7	-5.3	-4.6	-4	-1.4	-7.6	4.1	0.5
17	-6.1	-5.5	-5.3	-4.7	-2.9	-2.4	-3.6	0.4	2
18	-8.3	-7.7	-3.4	-4.7	-3	-1.2	-7.7	2.5	-1.3
19	-2.2	-1.2	-4.8	-7.6	-0.5	-9.5	-5.8	-5.7	-2.3
20	-4.8	-11.9	-10.7	9.1	-3.3	-5.4	13.3	2.1	2.1
21	-3	-5.7	-3.2	6	4.1	0.4	2.2	0.7	-4.4
22	-2.2	-4.9	-2.1	0.8	-2.1	-2.6	-0.6	-1.5	-4.1
23	-12.6	-13.7	-17.5	22.3	14.6	20.5	5.3	5.6	4.4
24	6.4	8.9	4	-3.1	2.8	4.2	-3.2	-3.5	-1
25	-6.7	-7.4	-9.6	4.9	5.9	-1.4	9.3	3.6	-4.9
26	15.7	16.3	13.6	-11.5	-9.3	-11.4	1.1	-1.3	0.8
LSD**									
P 5% ±	4	5	5	4.7	5.7	6.5	6.1	3.1	4.3
P 1% ±	5.2	6.6	6.6	6.1	7.5	8.6	8	4.1	5.6
P 0.1% ±	6.7	8.5	8.5	7.9	9.7	11	10.3	5.3	7.2
CV%***	4.5	5.7	5.7	6.3	8	9.2	8.4	4.3	4.8

*, For explanation of codes see Table 31.
**, Least significant differences as percentages of the Grand Means.
***, Coefficient of variation percentages.

TABLE 33 : Percentage differences in morphometric means of X. diversicaudatum (n=5) males from different populations.

POPULATIONS*	L	ANT o/i junc	TES-TES	TAIL	SPIC-ULA	ODONTO style	ODONTO phore	SPEAR
Grand Means	4.58	498	2.68	49.8	68.8	130.3	78.8	209.1
1	20.5	6.8	11.5	-4.5	16	5.9	4.9	5.5
2	-4.7	-0.7	-12.9	0.7	-0.6	-1.9	1.1	-0.8
3	2.5	4.9	1.2	-0.1	6.4	0.5	4.1	1.9
4	19.3	8.1	21.7	0.3	6.4	7	2.8	5.4
5	11.7	14.1	21.3	18.8	10.4	18.3	14.5	16.9
6	5.1	4	5.8	-3.9	1.7	4.3	1.3	3.2
7	-9.1	1.1	-5.4	-9.3	-5.3	-1.5	-0.7	-1.2
8	-15.3	2.1	-12.8	-10.5	4	-1	-2	-1.4
9	13.9	9	16.5	3.9	6.4	5.6	7.7	6.4
10	6.2	1.1	9.6	-5.7	1.7	-0.3	-1.5	-0.7
11	-6.2	3.1	-10.9	-9.8	-5.3	0.5	1.1	0.7
12	11.7	4	0.3	1.1	4	4.5	5.6	4.9
13	11.7	4.4	14.2	-1.3	4	5	-0.2	3
14	-9.5	-9	-7.1	5.5	-7.6	-12.7	-9.1	-11.3
15	-6.9	-6.6	-1.8	7.5	-2.9	-5	-5.8	-5.3
16	-6.8	-7.6	-1.6	-2.1	-2.9	-4.6	-2.2	3.7
17	-18.7	-9.9	-20.3	-6.1	-7.6	-5.8	-7.6	-6.5
18	-10.6	-7.6	-18.5	3.9	-9.9	-6.4	-4.8	-5.8
19	-13.4	-9.9	-7.1	1.1	-9.9	-11.3	-7.1	-9.7
20	5.1	4	4.9	1.9	-2.9	0	2.3	-0.9
21	-11.3	-8.1	-7.2	-3.3	1.7	-5.5	-4.5	-5.1
22	-8.4	-10.4	-12.7	2.7	-9.9	-4.9	-5.5	-5.1
23	13.9	-11.3	11.5	-9.7	-12.2	-2.4	-8.6	-4.7
24	1.2	3.5	-5.3	-2.1	2.9	1.6	5.9	3.2
25	-0.8	-3.8	2.1	0.7	4	-5	-2.5	-4.1
26	-1.4	15	3	12	7.5	15.1	11	13.5
LSD**								
P 5% ±	9.3	7.2	14.5	9.1	8.7	4.3	5.4	2.1
P 1% ±	12.3	9.5	19	11.9	11.4	5.6	7.2	2.7
P 0.1% ±	15.9	12.3	24.6	15.4	14.8	7.3	9.2	3.5
CV%***	7.4	5.8	11.6	7.2	6.9	3.4	4.3	2.8

*, For explanation of codes see Table 31.
**, Least significant differences as percentages of the Grand Means.
***, Coefficient of variation percentages.

TABLE 33 : continued.

POPULATIONS*	WIDTHS			RATIOS					
	spear base	great	anus	a	b	c	c'	S	T
Grand Means	44.7	54	43.5	85.4	9.21	92.4	1.15	4.7	58.6
1	3.4	9.6	6.1	9	13	25.4	-10.6	1.6	-7.5
2	-2.9	-11.1	-0.3	6.5	-4.2	-5.5	0.6	1.9	-8.8
3	3.8	2.2	2.4	-0.4	-2.3	2	-3.1	-2.2	-1.4
4	2.5	2.6	7	15.4	9.9	18.7	-6.8	2.4	2.3
5	37.8	48.8	38.3	-25.4	-2.2	-6.1	-14.5	-15.2	8.4
6	3.4	6.3	6.6	-1.7	0.9	0.7	-3.2	-0.5	0.1
7	-5.6	-6.3	-7.2	-3.7	-10.4	0	-2.8	4.4	4
8	-2.9	0	6.6	-16.5	-17.6	-6.3	-16.6	1.2	2
9	3.4	4.4	4.3	8.1	4.3	9.8	-0.6	2.5	2.1
10	5.2	4.4	3.4	1.2	4.7	12.4	-9.3	-5.9	3.2
11	-2	6	-5.8	-0.9	-9.2	3.2	-4.7	2.4	-4.9
12	2.5	7.7	7	2.9	7.4	9.6	-6	2	-10.4
13	5.2	5.1	-1.2	5.3	7	12.8	0.7	-2.1	1.7
14	-6.5	-6.7	-4.9	-3.9	-0.9	-13.8	10.5	-5.6	2.7
15	-8.3	-9.3	-8.1	1.9	-0.4	-13.7	16.4	2.8	5.3
16	-9.2	-9.7	-8.1	2.3	0.4	-5.4	6.1	5.7	5.7
17	-8.7	-11.1	-10.9	-8.8	-9.4	-13.4	4.7	2.1	-2.2
18	-8.7	-6.7	-2.6	-5.1	-3.5	-14.7	6.2	3.2	-8.9
19	-5.6	-8.6	-9	-6.2	-4	-13.9	10.4	-4.7	7.2
20	1.6	-7.4	-3.5	12.8	0.9	3.2	5.2	-1	-0.5
21	-10	-11.5	-7.7	-0.5	-2.5	-7.8	3.9	-5	4.9
22	-5.1	-6.7	-5.8	-2.7	2.2	-11.3	8.5	-0.3	-4.6
23	-8.7	-14.1	-13.6	31.4	29.4	25.5	4	3.9	-1.8
24	3.4	4.4	1.5	-3.9	-2.4	-2.7	-4	-0.4	-6.1
25	-1.2	-6.3	-4.5	5.1	3.4	-1.8	4.8	-3.3	2.6
26	13.2	25.9	10.2	-22.2	-14.5	-2.3	1.7	0.1	4.7
LSD**									
P 5% ±	5.5	7.5	5.6	4.3	5.8	6.9	5.9	3.1	10.7
P 1% ±	7.3	9.9	7.3	5.7	7.6	9	7.7	4	14.1
P 0.1% ±	9.4	12.7	9.5	7.3	9.8	11.6	9.9	5.2	18.3
CV%***	4.4	6	4.4	6.3	8	9.2	8.4	4.3	8.6

*, For explanation of codes see Table 31.
**, Least significant differences as percentages of the Grand Means.
***, Coefficient of variation percentages.

TABLE 34 : The number and significance of some morphometric differences present in females from populations of X. diversicaudatum when compared with the Grand Means obtained for all the populations studied.

X. diversicaudatum population*	Number of morphometrics significantly different from the Grand Means. P less than 5%	P less than 1%	P less than 0.1%
2	2	0	0
11	2	0	0
10	4	0	0
7	6	0	0
21	3	1	0
22	4	2	0
24	6	3	1
13	7	4	1
3	6	2	2
6	6	3	2
17	11	6	2
25	12	7	2
12	9	6	3
20	5	4	4
1	10	7	4
8	6	5	5
19	10	9	5
9	11	9	5
16	13	8	5
14	13	10	5
18	12	8	6
4	15	11	6
15	11	8	7
26	11	11	9
5	13	12	11
23	16	15	14

*, For explanation of codes see Table 31.

TABLE 35 : The number and significance of some morphometric differences present in males from populations of X. diversicaudatum when compared with the Grand Means obtained for all the populations studied.

X. diversicaudatum populations	Number of morphometrics significantly different from the Grand Means. P less than 5%	P less than 1%	P less than 0.1%
3	0	0	0
24	2	1	0
6	3	1	0
11	3	1	0
2	2	2	0
20	1	1	1
25	4	1	1
7	5	2	1
13	6	2	1
12	9	2	1
21	8	4	1
22	8	4	1
10	3	3	2
16	8	4	2
18	11	4	2
9	8	6	2
8	6	4	3
15	8	5	3
19	13	9	4
14	9	6	5
4	10	7	5
17	12	12	5
23	13	11	6
1	10	8	7
26	10	10	9
5	14	12	11

*, For explanation of codes see Table 31.

TABLE 36 : "Importance values"* for five variates used in canonical variate analysis of 26 populations of X. diversicaudatum

Canonical variate	Axis		
	1	2	3
L	-0.2173	-1.2142	-0.0648
V	0.0218	-0.2739	0.0788
c'	-0.0817	0.0662	0.9903
Odontostyle	1.4930	0.1555	0.5084
Odontophore	0.7714	0.6490	-0.1011

*, "Importance value" = CVA loading X SD of variate.

TABLE 37 : Morphometrics of female X. diversicaudatum (n=10) from seven field populations and from specimens from the same populations but obtained four years after the populations were placed in a heated glasshouse.

Population*	♀	YEAR	L	ANTERIOR vulva	ANTERIOR o/i junc	TAIL	WIDTH great anus	WIDTH anus	ODONTO style	ODONTO phore
			(mm)	(mm)	(um)	(um)	(um)	(um)	(um)	(um)
Pop.14 (field)		1978	4.30	1.86	467.2	53.2	55.5	41.1	120.4	74.9
(glasshouse)		1981	4.64	2.01	492.5	55.7	59.8	42.2	132.6	82.9
Pop.15 (field)		1978	4.30	1.84	459.1	50.9	54.1	38.6	124.2	75
(glasshouse)		1981	4.07	1.77	448.2	55.5	58.1	40.4	127.4	78.8
Pop.17 (field)		1978	4.24	1.83	469.6	44.6	56.3	41.8	125.4	74.3
(glasshouse)		1981	3.91	1.70	451.3	49.6	57.4	43.5	127.5	79.4
Pop.20 (field)		1978	4.53	1.95	502.8	49.3	52.5	39.4	129.6	77.9
(glasshouse)		1981	4.37	1.85	482.9	53.5	63.7	45.4	134.8	82.6
Pop.21 (field)		1978	4.70	1.90	487.2	48.2	56.2	42.7	129.3	77.7
(glasshouse)		1981	4.51	1.88	500.7	53.2	64.4	47.5	137.2	82.6
Pop.24 (field)		1978	4.96	2.07	518.8	49.1	64.9	45.9	136.1	81.1
(glasshouse)		1981	4.52	1.94	496.7	52.4	65.7	47.4	136.3	87.5
Pop.25 (field)		1978	4.58	1.84	464.9	48.0	55.2	39.9	125.8	78.8
(glasshouse)		1981	4.39	1.82	490.4	55.1	61.3	45.4	134.5	85.2
LSD	5%		0.31	0.20	26.1	4.3	3.2	2.1	4.8	3.7

*, For explanation of codes see Table 31.

TABLE 38 : Morphometrics of male X. diversicaudatum (n=5) from seven field populations and from specimens from the same populations but obtained four years after the populations were placed in a heated glasshouse.

POPULATION*	YEAR	L	TES-TES	ANT o/i junc	TAIL	WIDTHS great	WIDTHS anus	ODONTO style	ODONTO phore
		(mm)	(mm)	(um)	(um)	(um)	(um)	(um)	(um)
Pop.14 (field)	1978	4.14	2.49	453.4	52.6	50.4	41.4	113.8	71.6
(glasshouse)	1981	4.51	2.73	497.2	54.8	55.8	42.8	134.4	80.8
Pop.15 (field)	1978	4.26	2.63	465	53.6	49	40	123.8	74.2
(glasshouse)	1981	3.96	2.38	457.6	59.4	53.2	41.8	126	77.6
Pop.17 (field)	1978	3.72	2.14	448.6	46.8	48	38.8	122.8	72.8
(glasshouse)	1981	4.22	2.6	469	50.8	55.4	44.4	134.6	82.4
Pop.20 (field)	1978	4.81	2.81	517.8	50.8	50	42	130.4	80.6
(glasshouse)	1981	4.43	2.99	505.6	56.4	61.8	46	135	82.8
Pop.21 (field)	1978	4.06	2.49	458	48.2	47.8	40.2	123.2	75.2
(glasshouse)	1981	4.41	2.69	477.4	56.8	60.2	44	131.4	84.2
Pop.24 (field)	1978	4.63	2.54	515.6	48.8	56.4	44.2	132.4	83.4
(glasshouse)	1981	4.68	2.88	476.8	55.6	62.4	47.4	139.4	85.4
Pop.25 (field)	1978	4.54	2.74	479	50.2	50.6	41.6	123.8	76.8
(glasshouse)	1981	4.39	2.78	503	54.6	58.6	47.6	136	85
LSD 5%		0.36	0.24	30.1	5	3.6	2.4	5.5	4.3

*, For explanation of codes see Table 31.

FIGURE 15 : Geographical locations of populations of X. diversicaudatum: 1, Dundee (field), Scotland; 2, Dundee (glasshouse), Scotland; 3, Cupar, Scotland; 4, Kilsyth, Scotland; 5, Ilkely, England; 6, Bury St. Edmunds, England; 7, Harpenden, England; 8, Aylesford, England; 9, High Halstow, England; 10, Treswithian, England; 11, Wrekin, Wales; 12, Nevern, Wales; 13, Saint-Katherina-Lombeek, Belgium; 14, Kostinbrod, Bulgaria; 15, Les Adrets, France; 16, Liguria region, Italy; 17, Lombardi region, Italy; 18, Piemonte region, Italy; 19, Wageningen, Netherlands; 20, Alexandra, New Zealand; 21, Sandefjord, Norway; 22, Rygge, Norway; 23, Cazalegas, Spain; 24, Holzieken, Switzerland; 25, San Diego, USA; 26, Nowy Sacz, Poland.

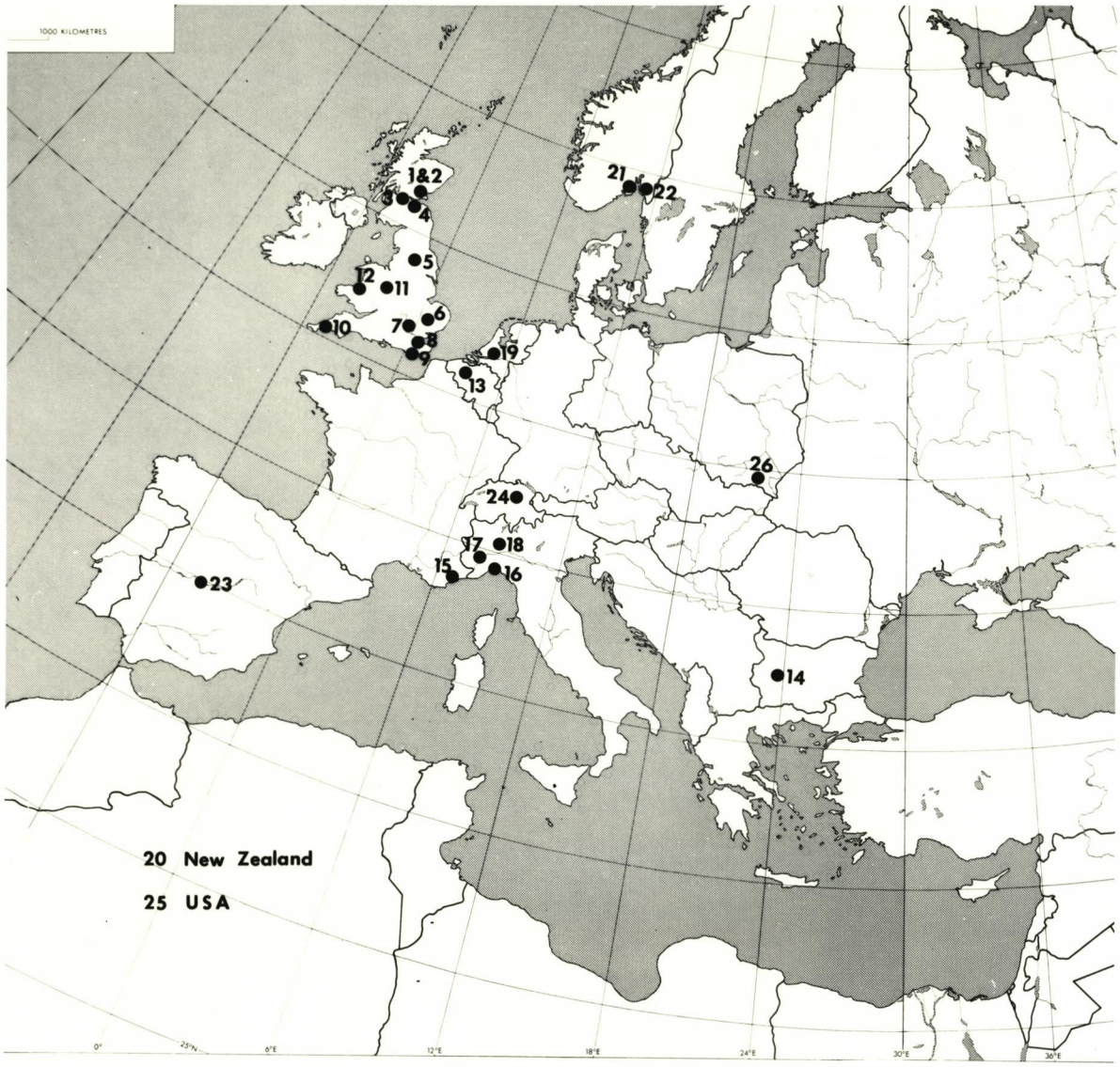

1000 KILOMETRES
1&2
4
5
12
11
6
7
10
8
9
19
13
21
22
26
24
17
18
15
16
23
14
20 New Zealand
25 USA
0°
25°N
6°E
12°E
18°E
24°E
30°E
36°E

Figure 16: Distribution of 26 populations of X.diversic-audatum relative to axes 1 & 2 of a CVA using the characters L, V, c', odontostyle and odontophore lengths. The 95% confidence radius for each population is 0·774. See Table 31 for key to population number code.

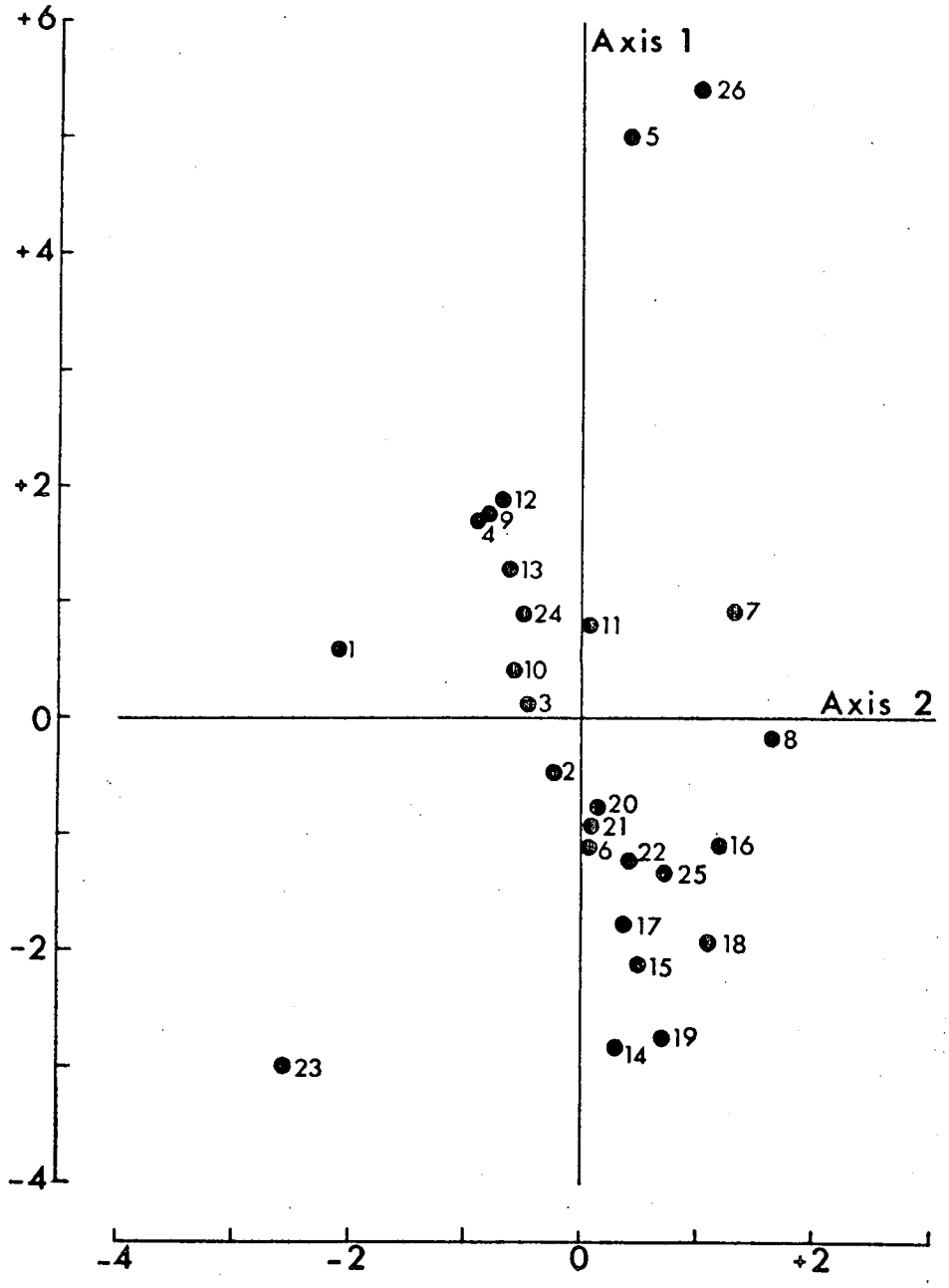


Figure 17 : As for Figure 16 but with axes 1 & 3.

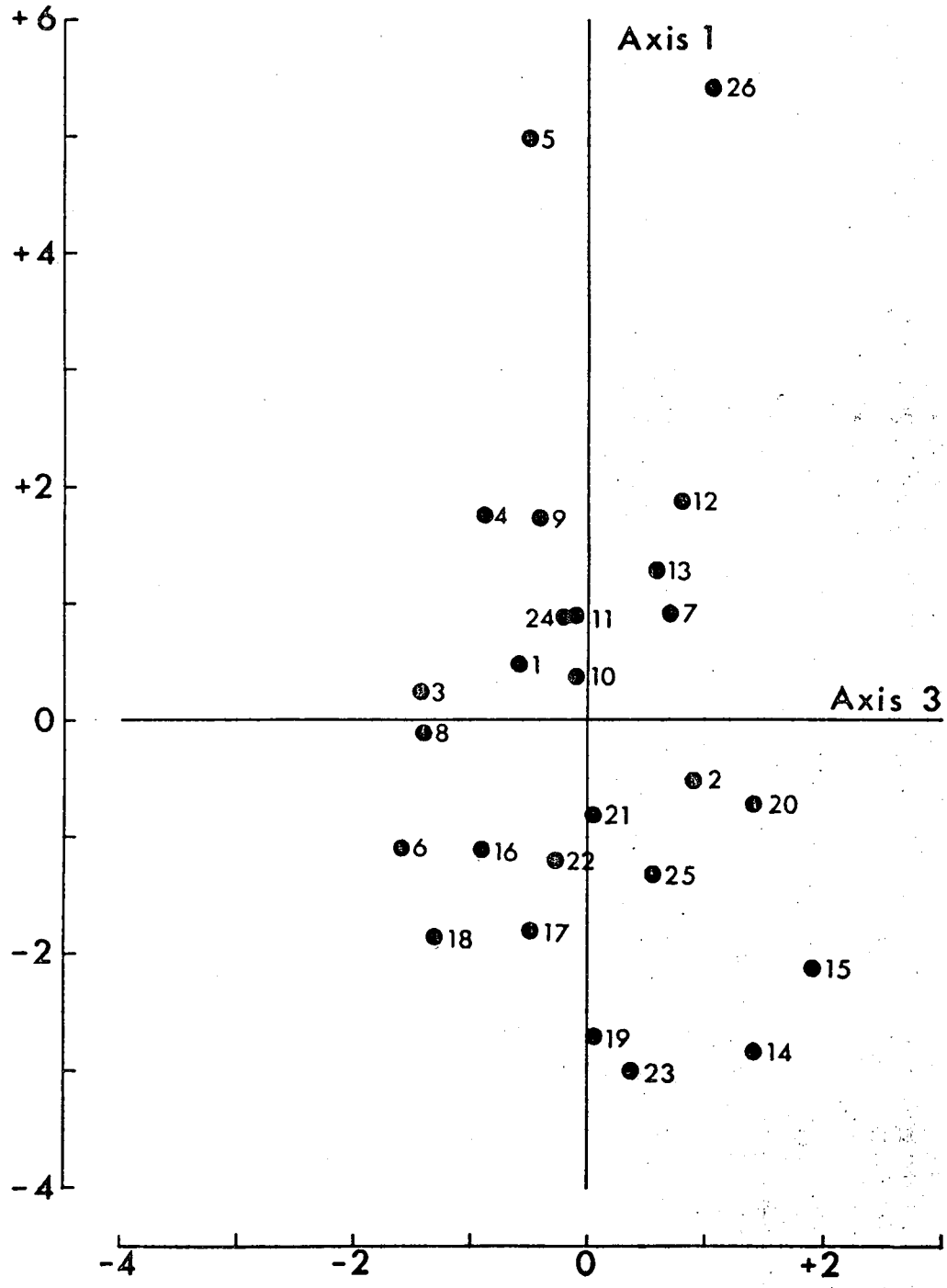


Figure 18: As for Figure 16 but with axes 2 & 3.

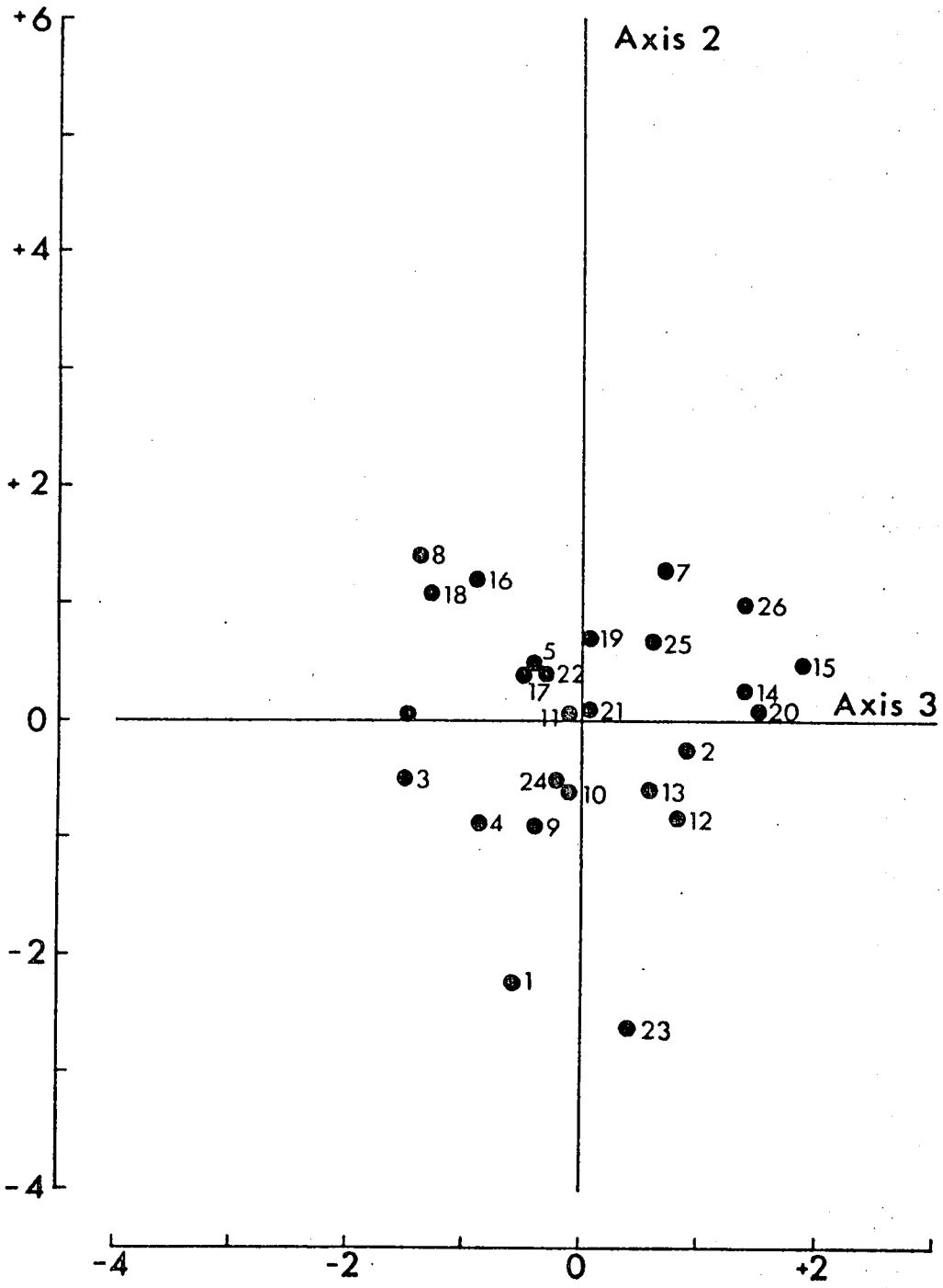


FIGURE 19 : Dendrogram showing the clustering of 26 populations of X. diversicaudatum at different levels of similarity as computed by canonical variate analysis of five morphometric characters. On the scale of similarity 100 = perfect similarity. For explanation of population code see Table 31.

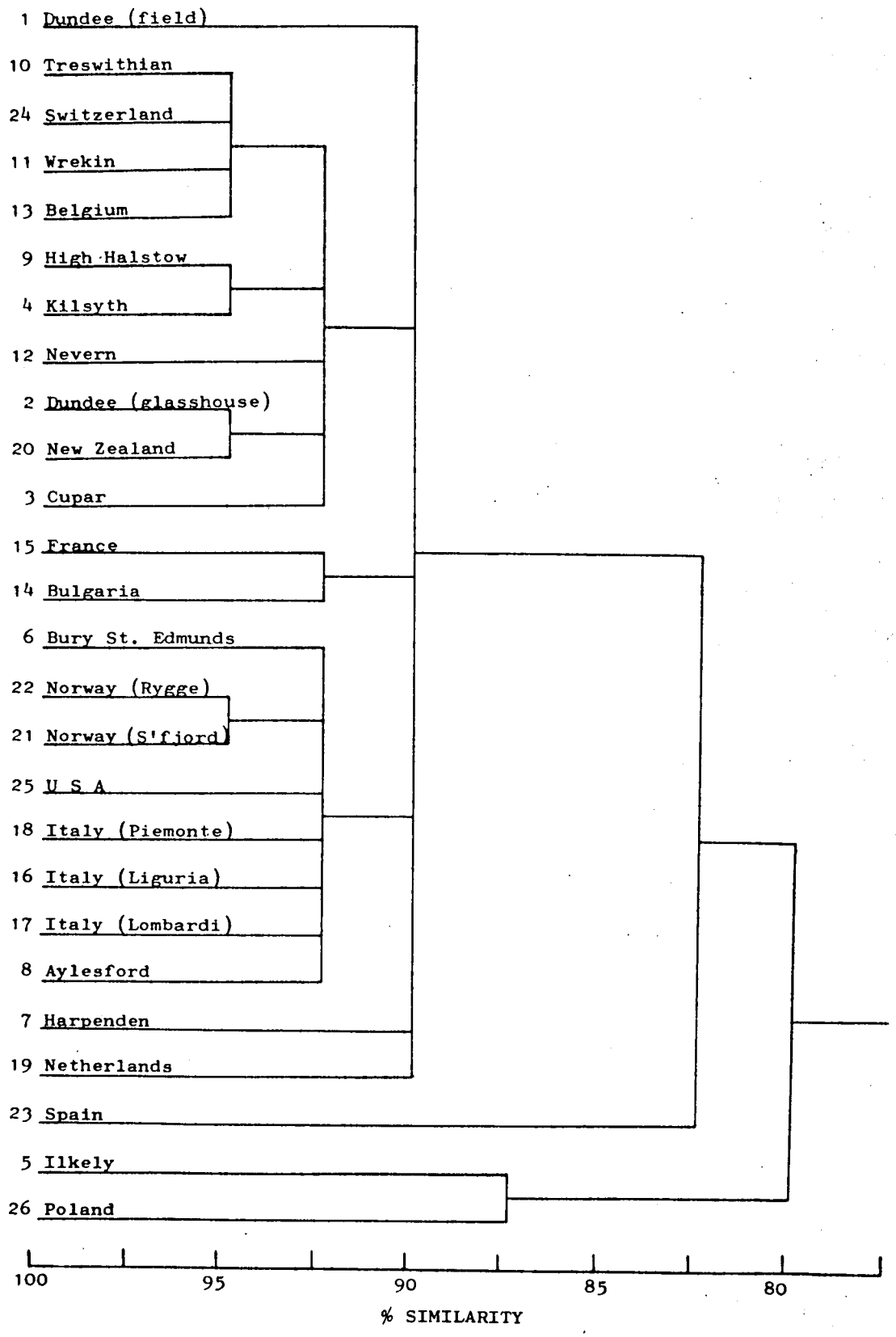

1 Dundee (field)
10 Treswithian
24 Switzerland
11 Wrekin
13 Belgium
9 High Halstow
4 Kilsyth
12 Nevern
2 Dundee (glasshouse)
20 New Zealand
3 Cupar
15 France
14 Bulgaria
6 Bury St. Edmunds
22 Norway (Rygge)
21 Norway (S'fjord)
25 U S A
18 Italy (Piemonte)
16 Italy (Liguria)
17 Italy (Lombardi)
8 Aylesford
7 Harpenden
19 Netherlands
23 Spain
5 Ilkely
26 Poland
100
95
90
85
80
% SIMILARITY

FIGURE 20 : A) A comparison of morphometric means a : largest values; b : standard treatment values; c : smallest values, obtained from female X. diversicaudatum prepared for examination by optical microscopy using different methods (see Chapter VII).

B) A comparison of morphometric means a : largest values; b : Grand Means; c : smallest values, obtained from female X. diversicaudatum from different populations.

The morphometric lengths are : 1) odontostyle; 2) odontophore; 3) spear; 4) anterior to oesophageal-intestinal junction; 5) anterior to vulva; 6) anterior gonad; 7) posterior gonad; 8) anterior to anus; 9) tail; 10) total body, and widths are : 11) at spear base; 12) at vulva; 13) at anus (see Chapter VII, Table 22).

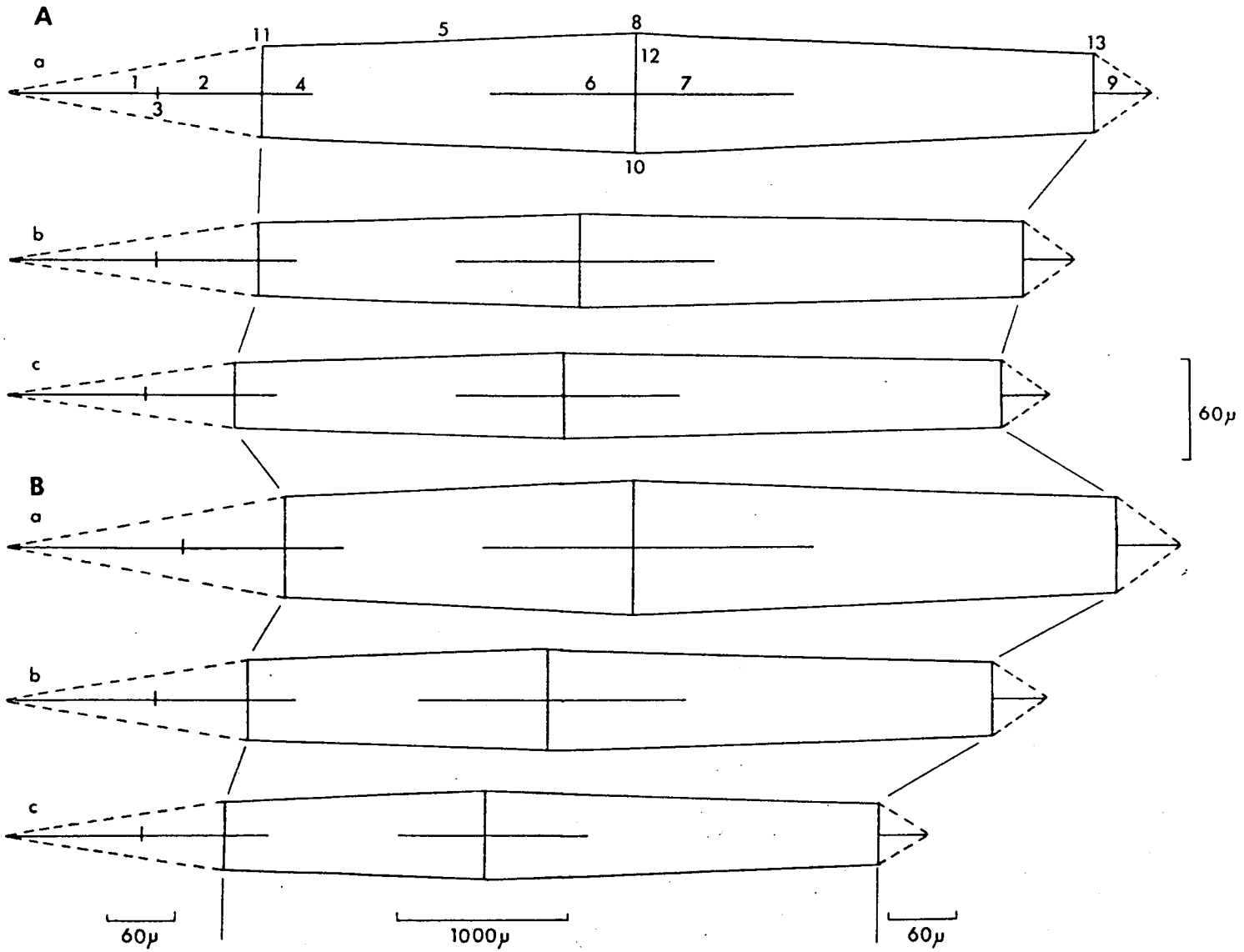
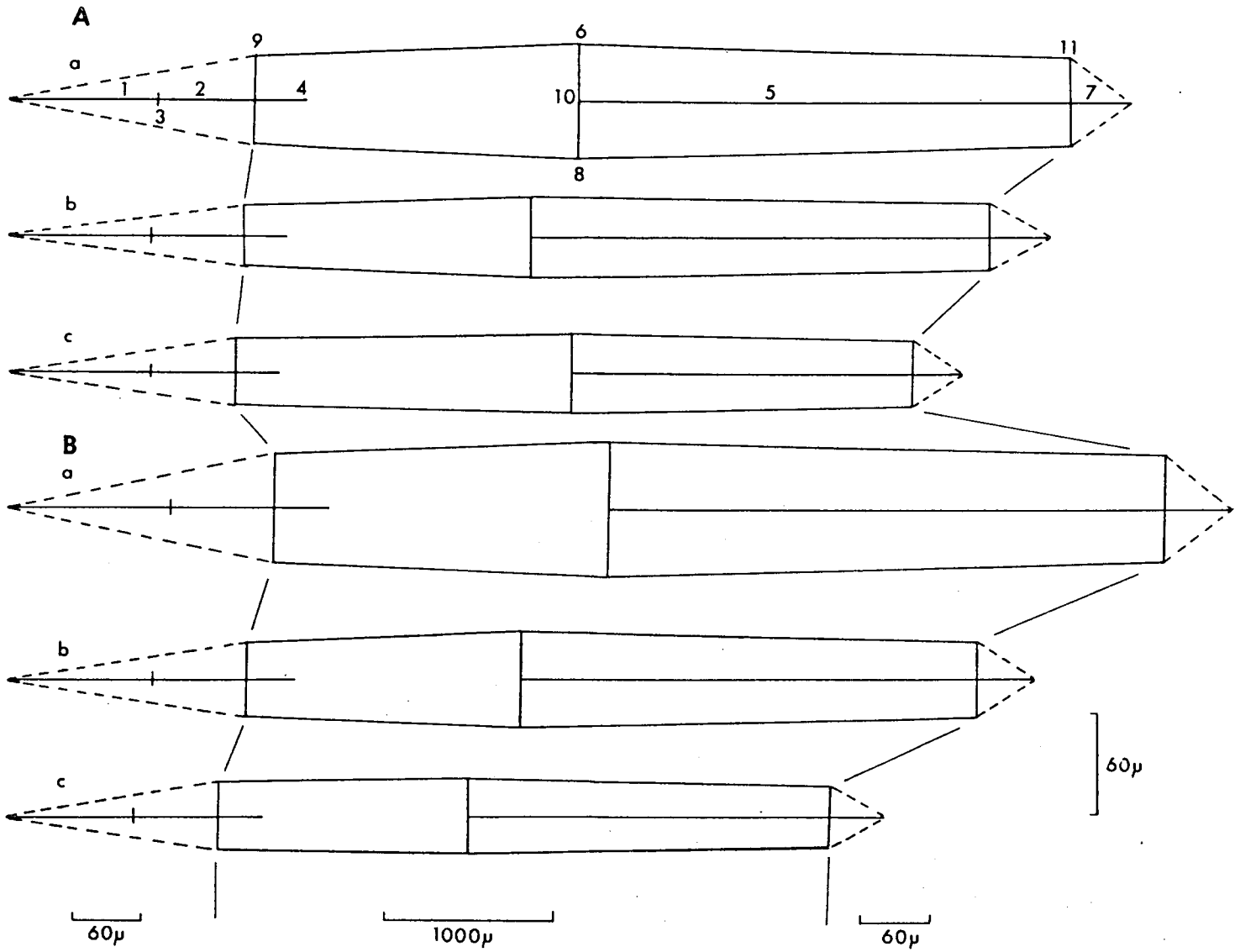

A
a
1
2
3
4
5
6
7
8
9
10
11
12
13
b
c
60μ
B
a
b
c
60μ
1000μ
60μ

FIGURE 21 : A) As for Figure 20A but for male X. diversicaudatum (see Chapter VII).

B) As for Figure 20B but for male X. diversicaudatum.

The morphometric lengths are : 1) odontostyle; 2) odontophore; 3) spear; 4) anterior to oesophageal-intestinal junction; 5) testes; 6) anterior to anus; 7) tail; 8) total body, and widths are : 9) at spear base; 10) greatest; 11) at anus (see Chapter VII, Table 22).


A
a
9
6
11
1
2
4
10
5
7
3
8
b
c
B
a
b
c
60μ
60μ
1000μ
60μ

PART THREE

"REPRODUCTIVE BIOLOGY"

CHAPTER IX

SEX RATIOS, REPRODUCTION AND CROSS-BREEDING WITHIN AND BETWEEN POPULATIONS OF XIPHINEMA DIVERSICAUDATUM

IX : 1 INTRODUCTION

The reproduction and life cycle of several Longidoroidea species are referred to in several publications. Many of these reports appear to contain somewhat inconsistent information. For example, the sex ratios of males to females from different populations of X. diversicaudatum have been recorded as 38% and 62% males and females respectively, (Sturhan, 1963c), 40% and 60% (Goodey, Peacock and Pitcher, 1961) and 50% and 50% (Flegg, 1968; Flegg, Baxendale and Popham, 1970). Also, Dalmasso, Munck-Cardin and Legin (1972) reported that a population of X. diversicaudatum from glasshouse roses from Antibes, France, unlike three other populations from France, appeared to reproduce parthenogenetically. Also, X. index has been reported, by different authors, to complete its life cycle from egg to adult in 22 to 27 days at 24 C (Radewald and Raski, 1962), 7 to 9 months at 20 to 23 C and 3 to 5 months at 28 C (Cohn and Mordechai, 1969, 1970) and 2 to 4 months at 20 to 22 C (Prota et al., 1977). However, the apparently conflicting results presented by these latter reports may be the result of different populations of X. index being used or different methods being employed in the various laboratories where the studies took place.

Most reports on the biology of longidoroid nematodes rely on data collected from field observations (Cotton, 1976; Flegg, 1968; Griffin and Darling, 1964; Taylor, 1967; Taylor and Murant, 1968; Taylor and Thomas, 1968; Thomas, 1969). Few laboratory studies have been done to examine the biology of longidoroid nematodes because of difficulties in rearing populations of the nematodes under artificial culture conditions (Cohn and Mordechai, 1969; Flegg, 1968; Griffin and Darling, 1964). In laboratory studies examining reproduction and life cycles of longidoroid nematodes, field soil containing the

nematodes being studied or suspensions of these nematodes placed in soils in which nematodes were absent have been used (Cotton, 1970, 1973; Cotton, Flegg and Popham, 1970; Flegg, Baxendale and Popham, 1970; Yassin, 1969). There have been few studies where single nematodes have been used but populations of X. index, which is a parthogenetic species, have been raised from single specimens (Dalmasso, 1970; Dalmasso and Younes, 1969; Wyss, 1978). Similarly, single pairs of X. diversicaudatum (one male plus one female), on strawberry, produced a mean of 6.3 eggs during a seven month period (Flegg, Baxendale and Popham, 1970).

The present study using culture techniques developed for the purpose, examined the male to female sex ratio within populations of X. diversicaudatum and the reproductive potential of female X. diversicaudatum from different populations. The reproductive capacity was also investigated of individual female X. diversicaudatum from different populations when crossed with males from a Scottish population.

IX : 2 MATERIALS AND METHODS

IX : 2 : 1 Populations of X. diversicaudatum

Populations of X. diversicaudatum used were: pop. 1, Dundee (field), Scotland; pop. 8, Aylesford and pop. 9, High Halstow, England; pop. 17, Lombardi region, Italy; pop. 15, Les Adrets, France; pop. 25, San Diago, USA; pop. 14, Kostinbrod, Bulgaria; pop. 20, Alexandra, New Zealand; pop. 21, Sandefjord, Norway; pop. 24, Holziken, Switzerland and pop. 23, Cazalegas, Spain. The populations were obtained from their field locations and kept as cultures as described in Chap. VIII:2:1.

Nematodes were extracted from the soils using the method of

McElroy et al. (1977). In the reproduction studies specimens were hand-picked and one pre-adult female or fourth stage juvenile and three males were used for each replicate. Those replicates used to examine the possibility of parthenogenesis occurring in the populations, consisted of one pre-adult female or fourth stage juvenile.

IX : 2 : 2 Sex ratios in populations of X. diversicaudatum.

From 10 populations of X. diversicaudatum 2 x 200 g soil samples were collected on eight occasions, at irregular intervals, during a four year period. The X. diversicaudatum populations were kept as cultures in a heated glasshouse (Chap. VIII:2:1) and on each sampling date the nematodes were extracted, identified as males, females and juveniles, counted and returned alive, to their original cultures. The sampling dates were 4th November, 1978; 31st March, 1979; 2nd June, 1979; 19th April, 1980; 16th December, 1980; 16th May, 1981; 31st October, 1981 and 16th April, 1982.

IX : 2 : 3 Plant hosts used for reproduction studies with X. diversicaudatum

Strawberry (Fragaria x ananassa Duch.) has been shown to be a suitable plant host for X. diversicaudatum and therefore, small strawberry plantlets were used in the present study. Also, three week old seedlings of Petunia hybrida Vilm. and one week old seedlings of Lolium perenne L. were used in an experimnt with X. diversicaudatum from Spain and Scotland.

The strawberry plantlets, free of pathogens, were produced by plant tissue culture techniques (Boxus, 1974). Stolon meristem tips were obtained from a healthy cv. Cambridge Favourite plant. The tips were cultured in a nutrient agar medium (Murashige and Skoog, 1962) to produce calluses which were allowed to multiply and shoots were

eventually produced from the calluses. Selected shoots were separated from the calluses and placed in nutrient agar until they initiated roots. Plantlets with similar development were chosen for use in the study.

The plantlets were grown in each test for 12 wk but at 6 wk after the commencement of each test each plantlet was trimmed leaving only the two youngest leaf-stalks. This ensured adequate root-growth for nematode feeding but prevented the plantlets from becoming too large for the 25 ml plastic-pots.

IX : 2 : 4 Culturing techniques used for reproduction studies with X. diversicaudatum

A prepared soil mix, with an aggregate and particle size of less than 1410 um and more than 149 um, consisting of a 3:1 mix of air-dried sand and steam-sterilised, air-dried loam was used in all the tests. This particular soil mix was found to be suitable for nematode activity, plant growth and facilitated nematode recovery upon completion of each test.

The tests were made using 25 ml plastic-pots, without drainage holes, containing prepared soil mix into which the hand-picked nematodes were placed together with a strawberry plantlet. The plastic-pots were plunged into moist sand contained in a plastic-box which was part of a temperature controlled cabinet (Taylor and Brown, 1974) and a plate-glass top covered the plastic box to help maintain a constant high humidity in the chamber. Temperature in the control cabinet was maintained at 18 C $\pm$ 1 C and supplementary mercury vapour lamps were used to maintain a 16 h day-length.

IX : 2 : 4 : 1 Reproduction by females from different populations of X. diversicaudatum

Twelve weeks after the commencement of each test the nematodes

present were extracted from each replicate. The roots of the plantlets were examined for the presence of root galls which were considered indicative of the nematodes having fed. After counting the nematodes present, the adults were removed and the larvae remaining were placed into clean plastic-pots, together with a new plantlet, and the pots returned to the temperature controlled cabinet.

The nematodes were re-extracted, after a further period of 12 wk, and males and any pre-adult female or fourth stage juveniles present were used in a second test. The second test was concluded after 12 wk and the nematodes present in each replicate were extracted, counted and the plantlet root systems examined for galls.

IX : 2 : 4 : 2 Reproduction by female X. diversicaudatum from different populations crossed with males from a Scottish population

The techniques used were similar to those described in Chap. IX : 2:3:1 but, in the first test of this study the male nematodes were from a Scottish population (Dundee, field). In the second test of this study the males and pre-adult females and fourth stage juveniles used were the progeny resulting from the mating of the original females, from the different populations, with the Scottish males.

IX : 2 : 4 : 3 Longevity and reproductive capacity of individual female X. diversicaudatum.

The total reproduction of individual female X. diversicaudatum was studied using the replicates containing Scottish males and Scottish pre-adult females or fourth stage juveniles (Chap. IX:2:3:1). The females, from those replicates where the original female used was recovered at the end of the first 12 wk period, were returned to clean plastic-pots. Three new Scottish male X. diversicaudatum and a new strawberry plantlet were added to each pot. After 12 wk the nematodes were extracted, counted and the

original females recovered were again returned to clean pots containing three new male nematodes and a new plantlet for a further 12 wk. The nematodes were again extracted and the procedure was repeated until eventually none of the original females were recovered from the pots.

IX : 3 RESULTS

IX : 3 : 1 Sex-ratios

Males are relatively common in populations of X. diversicaudatum and generally account for 40 to 50% of a population. However, when populations of X. diversicaudatum were received at the SCRI, the ratio of males to females was found to differ between populations. The numbers of males and females present in ten populations kept as cultures at the SCRI were observed and counted on eight occasions, at irregular intervals during four years.

The proportions of males and females present in each population remained relatively constant during the four years of the study (Tab. 39). The differences between the largest and smallest values obtained for the proportions of males and females present within each population over four years was less than 10%. Except for pops. 1 and 15 which had 14% and 13% differences respectively between the largest and smallest values. Also, pop. 17 had a 25% difference between the largest and smallest values obtained for its males and females but much of this difference could be attributed to an unusually large percentage (72%) of females present in the final sample examined. Generally populations had 40% to 50% males present but, pops. 24 and 21 had 55% and 61% males present respectively, and pops. 20 and 25 had only 36% and 37% males present respectively.

IX : 3 : 2 Reproduction within populations

Females from all of the populations produced juveniles under the

test system used in the study. However, much variability was recorded in the number of juveniles produced by individual females from the same population. Also, similar variability was recorded in the mean numbers of juveniles produced by females from the different populations. The above applied both to the first and the second generations of juveniles (Tab. 40).

The mean numbers of juveniles produced by females from each population were relatively similar for the first and second generations although there was a trend towards higher numbers of juveniles in the second generation. For example, the mean numbers of second generation juveniles for pops. 14 and 20 were almost double the mean numbers of first generation juveniles (58 vs 35 and 55 vs 27 respectively). In contrast, the mean number of first generation juveniles for pop. 25 was double the mean number of second generation juveniles (52 vs 23).

The average of the mean numbers of first generation juveniles for pops. 1, 14, 17, 20, 21 and 24, whose individual mean numbers ranged from 27 to 39 per female, was 31. Similarly, for pops. 8, 13 and 15, whose individual mean numbers ranged from 6.5 to 12, the average was 9 and pop. 25 had the largest mean number with 52 first generation juveniles. For the second generation juveniles the average of the mean numbers for pops. 1, 17, 21, 24 and 25, whose individual mean numbers ranged from 23 to 49 per female, was 34. The average mean number for pops. 8, 13 and 15, whose individual mean numbers of second generation juveniles ranged from 10 to 11, was 10.5. Pops. 20 and 14 had the largest mean numbers of second generation juveniles with 55 and 58 respectively.

Only two females from pop. 23, from Spain, produced first generation juveniles which were too few to be used to provide

meaningful information on the production of second generation juveniles. The reproductive ability of females from this population was further examined in separate tests and the results of these tests are presented in a subsequent chapter.

In a series of replicates corresponding to the reproductive study but with each replicate containing only a single fourth stage juvenile most of the juveniles developed into females. None of the females became gravid indicating that parthogenesis is unlikely to occur in any of the populations used in the study.

IX : 3 : 3 Reproduction of females from populations when mated with males from a Scottish population

Under the test system used in the study some females from all the populations, when mated with males from a Scottish population, produced juveniles (Tab. 41). Furthermore, the first generation juveniles were found to be reproductively viable and produced second generation juveniles. Also, as found in the study of reproduction with various populations much variability was recorded in the number of juveniles produced by individual females from the same population and in the mean numbers of juveniles produced by females from the different populations. The above applied both to the first generation crossbred juveniles and to the second generation juveniles produced from the crossbred populations.

The average mean number of first generation juveniles produced by females from pops. 14, 15, 17, 20 an 21, whose individual mean numbers ranged from 33 to 64, was 47. Whereas, the average mean number for pops. 8, 13, 24 and 25, whose individual mean numbers ranged from 11 to 21, was 17. The average mean number of second generation juveniles produced by crossbred females from all the populations was 39. The individual mean numbers of juveniles produced

by the crossbred females used from the different populations appeared to form a more continuous range, 25 to 62, than did the corresponding values obtained from the original maternal females.

Generally, the crossbred females produced larger mean numbers of juveniles than did their original maternal females except in pops. 14, 15 and 17 where the maternal females produced larger mean numbers of juveniles than did the resulting crossbred females. The crossbred females produced from 0.25 (pop. 20) to 3 (pop. 25) times larger mean numbers of juveniles than did their maternal females; whereas in pops. 14, 15 and 17 the numbers were 0.25 to 0.5 times less than the mean numbers of juveniles produced by the maternal females.

Four juveniles were produced by only one female from pop. 23 and these were insufficient to study their reproductive viability. However, the ability of this population to crossbreed with a Scottish population was further examined in tests using different plant species and the results are reported in the following section.

IX : 3 : 4 Reproduction of females from a Spanish population on three plant species and ability to crossbreed with males from a Scottish population.

As stated in the preceding sub-chapter very few females from pop. 23 produced juveniles on strawberry host plants. Therefore, Petunia hybrida and Lolium perenne plants were examined as hosts for nematodes from pops. 1 and 23. Females from pop. 1 produced similar numbers of juveniles on P. hybrida as they did on strawberry but produced only a few juveniles on L. perenne (Tab. 42). Only one female from pop. 23 reproduced on P. hybrida and none reproduced on L. perenne plants. The single female from pop. 23 which reproduced on P. hybrida produced substantially more juveniles than the two females which reproduced on strawberry (13 vs 2.5 juveniles respectively).

No reproduction occurred on P. hybrida and L. perenne in those replicates containing a single female from pop. 23 together with three males from pop. 1.

IX : 3 : 5 Longevity and total reproductive capacity of individual females from a Scottish population.

During the first 12 wk period of this test 12 of the original 20 juveniles moulted to females which were subsequently fertilized by the males and produced a mean of 39 juveniles (range 34 to 47 juveniles). Of the remaining eight, four became males, two were not recovered and two had become females and had produced a few juveniles, but also were not recovered. After 24, 36 and 48 wk four, three and two females were not recovered. The results were not used from these replicates as the females had reproduced only a few juveniles during the 12 wk prior to their non-recovery at an extraction date (Tab. 43).

At 24, 36 and 48 wk eight, five and three females produced means of 68 (58 to 83), 34 (20 to 43) and 21 juveniles (13 to 28 juveniles). Also, at each extraction date except 48 and 60 wk many of the females were gravid and the juveniles recovered comprised only first, second and third stages. Females at 12, 24 and 36 wk and males, used for the study, had dark, opaque bodies but females remaining at 48 and 60 wk had clear, translucent bodies and moved sluggishly.

IX : 4 DISCUSSION

The present study has established that differences occur in the sex ratios between populations of X. diversicaudatum as has been reported by Flegg (1968); Flegg, Baxendale and Popham (1970); Goodey, Peacock and Pitcher (1961); Sturhan (1963c) and by Triantaphyllou (1973) for several other spp.

Such differences possibly reflect survival strategies adopted by

the X. diversicaudatum populations as a result of biotopic conditions. As longidoroid nematodes, particularly X. diversicaudatum, appear to have relatively long life spans adaptive changes in the sex ratio in these nematodes, brought about by changes in their biotopes, may take several years to accomplish. Therefore, it may not be possible to observe such changes during the four years in which the present study was undertaken. However, the final sampling of a X. diversicaudatum population from Lombardi region, Italy revealed an unusually large proportion of female nematodes (72%). It is possible that this change in the proportion of male and female nematodes from this population was an indication that the sex ratio was changing in favour of females, such a change possibly having been induced by changes in the biotope.

Methods adopted in the present study, to examine reproduction by individual females from several populations of X. diversicaudatum appear to have overcome many of the problems reported by earlier workers (Cohn and Mordachi, 1969; Flegg, 1968; Griffin and Darling, 1964). Differences were found to occur in the reproductive ability of individual females from the different populations studied and parthenogenesis was not found to occur in any of the populations studied. Using a standard culture technique e.g. plant, temperature, soil characteristics, soil moisture and lighting, for reproduction by individual nematodes from the populations the results obtained were comparable. The results suggested that the populations could be placed into arbitrary groups based upon the mean reproductive rates of the females. For example, based on first generation reproductive means, pops. 1, 14, 17, 20, 21 and 24 formed a group (reproductive mean c. 30) whereas, based on second generation reproductive means pops. 1, 17, 21 and 24 formed a group (reproductive mean c. 35) and pops. 14 and 20 formed a second group (reproductive mean c. 57).

In all cases, except one, where females from the X. diversicaudatum populations were mated with males from a Scottish population (pop. 1) the females became gravid, produced juveniles and these juveniles were reproductively viable. Females from a Spanish population (pop. 23) were the exception; only one female became gravid and produced a few juveniles. Because of the small number of juveniles produced by this female it was not possible to establish if the juveniles were reproductively viable. As in the study examining reproduction within populations it was possible again to establish groups of populations based on their reproductive means. Also, these new groups of populations could be increased in number depending on the reproductive ability of the crossbred juveniles.

Differences in the reproductive abilities of females from various populations probably reflect differences in their biotopes. Some populations probably have a higher optimum temperature requirement for reproduction and thus the temperature 18 C used may be more suitable for some populations than for others. Similarly, strawberry may be more suitable as a host for some populations. Coiro and Brown (1983) have shown that the host plant can affect the reproductive rate of populations of X. index by slowing the development of the nematodes. Temperature, rather than host, may be the factor which affected reproduction by individual nematodes from pop. 23 because, in general, fewer of the juveniles developed into adults than did juveniles from the other X. diversicaudatum populations. Increasing the temperature to more accurately reflect summer soil temperatures from central Spain, the origin of the populations, may allow the development and reproductive rate of nematodes from this population to be increased.

Crossbred females generally had a greater reproductive capacity

than did females from the original maternal population. However, much variability was evident in the numbers of juveniles produced by the individual females in this study. Therefore, the increases in the reproduction by the progeny of the crossbred females requires confirmation. It may then be possible to show that these progeny have become physiologically better adapted to reproduce on the host at the given temperature.

The numbers of juveniles recovered from each female were probably incomplete as some loss of juveniles may have occurred during the extraction procedure. Also, unhatched eggs were not recovered. If it is assumed, in the study examining the total reproductive capacity of individual X. diversicaudatum, that between 10% and 20% losses occurred the estimated reproductive capacity for each nematode is 180 to 200 juveniles. Little information, however, is available about the total reproductive capacity of plant parasitic nematodes. Croll and Matthews (1977) reported that the average number of eggs per female for Meloidogyne javanica was 350, for Anguina agrostis 1000 and for Globodera rostochiensis 200.

The values obtained for the total reproductive capacity of individual X. diversicaudatum may be atypical as only three females from the Scottish population, pop. 1, were considered to have completed their life span. Nevertheless, the similarity of the results obtained for the three nematodes suggests that the value obtained is representative of the populations.

No periodicity occurred in juvenile production which confirms that plant root production is probably a limiting factor to reproduction by the nematodes under field conditions (Flegg, 1968). X. diversicaudatum in southeastern England are reported to take two years to develop from eggs to adults and have a life span of three to

five years ibid. In the present study third stage juveniles were recorded 12 wk after fourth stage juveniles were placed in pots with host plants. Therefore, the time taken to complete one generation on strawberry at 18 C was slightly more than 12 wk, which is equivalent to more than 1,500 day degrees. The reproductive span of the Scottish females was c. 36 wk. equivalent to 4536 day degrees and the longevity of these females was c. 60 wk equivalent to 7560 day degrees.

Flegg, Baxendale and Popham (1970) suggested that X. diversicaudatum females produce between 10 and 20 eggs each year. These values, multiplied by the life span minus the egg to adult time given by Flegg (1968) suggest that the total reproductive capacity of X. diversicaudatum is between 10 and 60 eggs. However, ibid suggested that the life span figures given should be regarded as conservative estimates.

The results obtained in the present study reveal that between 12 and 36 wk Scottish females produced a mean total of 104 juveniles which was equivalent to a juvenile per 22 day degrees above a daily threshold temperature of 5 C. Cotten and Roberts (1980) reported a yearly mean of c. 1500 accumulated day degrees above 5 C in southeastern England. At 5 C or lower X. diversicaudatum eggs do not hatch (Flegg, 1969). Therefore, using these results, X. diversicaudatum females can be calculated as having, in Britain, a yearly production of 68 juveniles and a reproductive span of three years. These results support the results of Flegg (1968) but not the results of Flegg, Baxendale and Popham (1970). However, pops. 8, 13, 15 and 23 were markedly different in their reproductive rates when compared with other populations which were similar to the Scottish population. These four populations, on strawberry in field

situations, probably require substantially more than 22 day degrees per juvenile produced. Pop. 8 is from southern England and therefore if this population had a similar reproductive capacity to the population used by Flegg et al (1970) this may explain the difference in the results obtained by ibid and those in the present study. Also, it appears that the reproductive rates of the populations are probably not correlated with climatic areas as might be anticipated using number of day degrees per juvenile produced.

The three female X. diversicaudatum from pop. 1, which appeared to complete their life cycles under the experimental conditions used in this study, also appeared to continuously produce juveniles. Therefore, it is concluded that the egg laying cycle of X. diversicaudatum is continuous when conditions are favourable but that the female nematode can probably produce only about 200 eggs during its life span. Flegg (1968) suggested that in southeastern England the production of eggs by X. diversicaudatum females corresponded to the seasonal cycle of root growth in host plants. The results from this study would appear to support ibid's suggestion.

Overall, the populations from different geographical origins, used in this study, were able, with varying abilities, to reproduce on strawberry. Furthermore, females from each of these populations were able to breed successfully with males from a Scottish population and their progeny were reproductively viable. The variability in the mean numers of juveniles produced by the individual female X. diversicaudatum from the several populations could be used to form groups of populations having similar reproductive capacities. However, only nematodes from a Spanish population, pop. 23, appeared to differ from other populations in their optimum temperature requirement for reproduction. It is possible that under some natural

conditions pop. 23 may be reproductively isolated, by its reproductive temperature requirement, from several other X. diversicaudatum populations.

Large morphometric differences have been shown to exist between many of the populations examined during this study. These differences have enabled populations to be alloted to morphometrically similar groups. Populations, representative of several of the morphometrical groups of populations, have been shown to interbreed with the Scottish population. Therefore, the populations would appear to comprise a classical biological species which is morphometrically variable.

IX : 5 CONCLUSIONS

1) Differences were present in the proportions of males to females in populations of X. diversicaudatum although generally males accounted for 40 to 50% of the adult nematodes. The differences were consistent during four years but in an Italian population the ratio changed in favour of females at the end of this period. Because of the relatively long life spans of longidoroid nematodes adaptive changes in their sex ratios, induced by changes in their biotope, may only become apparent after several years.

2) It is estimated that a X. diversicaudatum female produces a maximum of 200 progeny each of which is produced every 22 day degrees above a daily threshold temperature of 5 C. Under test conditions reproduction was continuous which confirms that plant root production is a limiting factor in reproduction by the nematodes in the field.

3) Groups of populations could be established based on differences in the mean reproductive rates of both first and second generation females. Geographical origin of the populations was not reflected in the composition of these groups. However, differences in the reproductive capacities are probably determined by different biotopic requirements for the populations.

4) Females from all populations produced viable progeny when crossbred with males from a Scottish population. The reproductive capacities of crossbred females were generally greater than those from the maternal populations. Therefore these progeny may have become physiologically better adapted to reproduce under the experimental conditions.

5) Few females from a Spanish population became gravid when mated with males from the same and a Scottish population; they produced few progeny and reproduction was not improved using different plant species. It is possible that this population requires a higher temperature for efficient reproduction and this could result in these nematodes being reproductively isolated from several other populations of X. diversicaudatum.

6) Parthenogenesis did not occur in populations of X. diversicaudatum and females produced viable progeny when crossbred with males from a Scottish population. Thus, the populations comprise one classical biological species (interbreeding and gene interchange between individuals). However, it is possible that a higher temperature

requirement for the Spanish nematodes indicates a diverging population which in the future may be referred to a new species as a result of complete reproductive isolation and morphological differences.

TABLE 39 : Mean* percentages of males and females present in ten populations of X. diversicaudatum

POPULATION**	PERCENTAGES***		Total adult
	females	males	nematodes
20	64 ± 2.6	36 ± 2.6	1773
	(60 - 67)	(33 -40)	
25	63 ± 2	37 ± 2	1533
	(60 - 66)	(34 - 40)	
15	61 ± 3.8	39 ± 3.8	1305
	(54 - 67)	(33 - 46)	
14	59 ± 1.8	41 ± 1.8	1270
	(56 - 64)	(36 - 44)	
1	58 ± 4.5	42 ± 4.5	1913
	(54 - 68)	(32 - 46)	
17	56 ± 7.3	44 ± 7.3	1293
	(47 - 72)	(28 - 53)	
8	49 ± 2.6	51 ± 2.6	1012
	(45 - 54)	(46 - 55)	
9	49 ± 2.4	51 ± 2.4	1256
	(44 - 52)	(48 - 56)	
24	45 ± 2.2	55 ± 2.2	1431
	(41 - 48)	(52 - 59)	
21	39 ± 1.7	61 ± 1.7	1110
	(37 - 41)	(59 - 63)	

*, Means derived from eight separate counts obtained at irregular intervals during four years.

**, For explanation of codes see Table 31.

***, Mean, one standard deviation (n-1) and range.

TABLE 40 : Mean rates of reproduction, after 12 wk under strawberry (Fragaria x ananassa) host plants, by individual females from 11 populations of X. diversicaudatum.

POPULATION*	NEMATODES/REPLICATE		Mean numbers of juveniles after 12 wk.	
	pre-adult females	males	Generations** first	second
1	1	3	39 (24 - 56)	40 (37 - 43)
8	1	3	9 (5 - 12)	10.5 (9 - 12)
13	1	3	6.5 (6 - 7)	10 (8 - 14)
14	1	3	35 (16 - 61)	58 (58 - 59)
15	1	3	12 (6 - 18)	11 (7 - 15)
17	1	3	32 (23 - 45)	49 (10 - 67)
20	1	3	27 (6 - 52)	55 (26 - 72)
21	1	3	27 (17 - 49)	27 (21 - 39)
23	1	3	2.5*** (2 - 3)	-
24	1	3	28 (6 - 47)	32 (5 - 51)
25	1	3	52 (37 - 66)	23 (10 - 50)

*, For explanation of codes see Table 31.
**, Males and pre-adult females which developed from the first generation were used in a test similiar to the first. Juveniles produced in the second test were considered the second generation.
***, Juveniles were recovered from only two females.

TABLE 41 : Mean rates of reproduction, after 12 wk under strawberry (Fragaria x ananassa) host plants, by individual females from ten populations of X. diversicaudatum when crossed with males from a Scottish population.

POPULATION*	NEMATODES/REPLICATE		Mean numbers of juveniles after 12 wk. Generations**	
	pre-adult females	males	first	second
8	1	3	11 (3 - 20)	28 (20 - 36)
13	1	3	18 (5 - 27)	30 (6 - 46)
14	1	3	64 (32 - 82)	33 (30 - 39)
15	1	3	36 (13 - 70)	25 (7 - 42)
17	1	3	53 (38 - 67)	40 (21 - 84)
20	1	3	47 (32 - 62)	62 (12 - 107)
21	1	3	33 (18 - 43)	48 (41 - 62)
23	1	3	4***	-
24	1	3	21 (8 - 35)	35 (23 - 49)
25	1	3	17 (16 - 18)	54 (35 - 73)

*, For explanation of codes see Table 31.
**, Males and pre-adult females which developed from the first generation were used in a test similiar to the first. Juveniles produced in the second test were considered the second generation.
***, Juveniles were recovered from only one female

TABLE 42 : Mean rates of reproduction, after 12 wk under three plant species, by individual females from two populations of X. diversicaudatum and the potential for crossbreeding between the two populations.

POPULATIONS*	NEMATODES/REPLICATE		Mean numbers of juveniles after 12 wk.		
	pre-adult males		Fragaria	Petunia	Lolium
	females		ananassa	hybrida	perenne
1	1	3	39	40	10
			(24 - 56)	(37 - 43)	(6 - 15)
23	1	3	2.5**	13***	5***
			(2 - 3)	-	-
23 (female)/ 1 (males)	1	3	4***	0	0

*, For explanation of codes see Table 31.

**, Juveniles were recovered from only two females.

***, Juveniles were recovered from only one female in each treatment.

TABLE 43 : The total reproductive capacity of individual female X. diversicaudatum, from a Scottish population, at 18 C under Fragaria x ananassa host plants.

Nematodes/replicate		Juveniles recovered (cumulative totals)					
pre-adult female	male	Week 12	24	36	48	60	72
1	3	Male	-	-	-	-	-
1	3	Male	-	-	-	-	-
1	3	Male	-	-	-	-	-
1	3	Male	-	-	-	-	-
1	3	0	-	-	-	-	-
1	3	0	-	-	-	-	-
1	3	2	-	-	-	-	-
1	3	8*	-	-	-	-	-
1	3	40	40	-	-	-	-
1	3	37	38	-	-	-	-
1	3	37	38	-	-	-	-
1	3	34	43*	-	-	-	-
1	3	45	106	106	-	-	-
1	3	38	115	115	-	-	-
1	3	41	99	103*	-	-	-
1	3	44	118	155	155	-	-
1	3	36	105	135	135*	-	-
1	3	35	118	138	151	151	-
1	3	38	95	135	163	163	163
1	3	47	109	152	175	175	175
MEAN		39	108	143	163	163	-

*, Results above the line in each column are not used in calculating the means.

PART FOUR

"VIRUS TRANSMISSION"

CHAPTER X

THE TRANSMISSION OF VIRUSES BY XIPHINEMA DIVERSICAUDATUM

X : 1 INTRODUCTION

The type-British strain of arabis mosaic virus (AMV-T) was first described by Smith and Markham (1944) and further serologically distinguishable strains, isolated from hops (AMV-H; Bock, 1966) and from a population of X. diversicaudatum from a deciduous woodland (AMV-W; Clark, 1976), have been described. All three AMV strains have been reported to be transmitted by X. diversicaudatum and, like its vector, AMV is widely distributed in Europe (Martelli, 1975, 1978; Murant, 1970; Novak and Lanzova, 1975; Saric and Velagic, 1980). Also, AMV has been reported from Canada (Stace-Smith in Murant, 1970). Japan (Iwaki and Kamuro, 1974), New Zealand (Thomas and Proctor, 1972) and the USA (Waterworth, 1975). X. diversicaudatum was first reported to be a vector of AMV by Jha and Posnette (1959) and Harrison and Cadman (1959).

Lister (1964) described the type-British strain of SLRV (SLRV-T) and reported its vector to be X. diversicaudatum. Isolates of SLRV present in other European countries (Cech et al., 1980; Corte, 1968; Credi et al., 1981; Lamberti et al., 1980; Lister, 1964; Martelli, 1975, 1978; Murant, 1974; Nemeth, 1980; Novak and Lanzova, 1975; Richter and Kegler, 1967; Vegetti et al., 1979), Canada (Allen, Davidson and Briscoe, 1970) and New Zealand (Fry and Wood, 1973), although in some instances differing from SLRV-T in symptomology in indicator plants, were all considered to be serologically

indistinguishable from SLRV-T. However, during the course of the present study Hanson and Campbell (1979) reported a serologically distinct strain of SLRV from parsley grown in the USA. Also, Belli, Fortusini and Vegetti (1981) reported a strain of SLRV from raspberries from Italy and originally this virus was reported to be similar to SLRV-T (Vegetti et al., 1979) although two years earlier Murant (unpublished) had identified the virus as being a serologically distinct strain of SLRV (A. F. Murant pers. comm.). The strain of SLRV from the USA was identified in parsley grown from seed imported from Europe and it is suggested that the virus may have been introduced to the the USA in the parsley seed (Hanson and Campbell, 1979).

As stated, AMV-T and SLRV-T have been reported to be transmitted by populations of X. diversicaudatum from several European countries and New Zealand. AMV-H and AMV-W have been reported to be transmitted by the same population of X. diversicaudatum from Kent, England (Valdez et al., 1974) and Harrison (1967) reported the simultaneous transmission of AMV-T and SLRV-T by one X. diversicaudatum. However, Taylor and Brown (1976) during a survey of the distribution of longidoroid nematodes in the British Isles found that only 18 of 325 populations of X. diversicaudatum were naturally infective with AMV and/or SLRV. Also, several reports exist of populations of X. diversicaudatum which apparently were unable to transmit AMV or transmited AMV less efficiently than other populations (Dalmasso, Munck-Cardin and Legin, 1972; Martelli, 1975, 1978).

Taylor and Robertson (1970) reported that electron microscopy of thin sections of X. diversicaudatum which had fed on plants infected with AMV showed that virus particles were retained as a monolayer, adsorbed on to the cuticle lining the lumina of the odontophore,

anterior oesophagus and oesophageal bulb. Robertson (1975) later reported a similar site of virus retention in X. diversicaudatum fed on plants infected with SLRV.

Several unsubstantiated reports have implicated X. diversicaudatum as a vector of brome mosaic (Schmidt et al., 1963), cherry leaf roll (Fritzche and Kegler, 1964), carnation ringspot (Fritzsche and Schmelzer, 1967) and raspberry ringspot viruses (Fritzsche and Kegler, 1968). McNamara (1978) reported that although a strain of raspberry ringspot virus (English strain; RRV-E) was recovered from the roots of bait plants exposed to X. diversicaudatum which had fed on RRV-E infected plants none of the bait plants was systemically infected with virus. It was assumed that the RRV-E detected in the tests came from the external contamination of the bait plant root systems caused by nematode faeces adhering to the external surfaces of the roots or from bodies of nematodes entangled in the root systems. After assessing published reports of virus transmission by longidoroid nematodes Trudgill, Brown and McNamara (1983) concluded that more than two-thirds of such reports provided inadequate evidence that the nematode was the vector. And, that with X. diversicaudatum only the transmission of AMV and SLRV had been adequately described.

The opportunity therefore, was taken to examine the transmission of strains of AMV and SLRV by several populations of X. diversicaudatum from Europe, New Zealand and the USA. Also, some factors affecting the transmission of these viruses and the transmission of AMV-T and strains of SLRV by reciprocal crossbreeds from an Italian and Scottish population were examined.

X : 2 MATERIALS AND METHODS

X : 2: 1 Populations of X.diversicaudatum.

Populations of X. diversicaudatum used were: pop. 1, Dundee (field), Scotland; pop. 5, Ikley, England; pop. 8, Aylesford, England; pop. 9, High Halstow, England; pop. 14, Kostinbrod, Bulgaria; pop. 15, Les Adrets, France; pop. 17, Lombardi, Italy; pop. 20, Alexandra, New Zealand; pop. 21, Sandefjord, Norway; pop. 23, Cazalegas, Spain; pop. 24, Holzieken, Switzerland; and pop. 25, San Diego, USA. The populations were obtained from their field locations and kept as cultures as described in Chap. VIII : 2 : 1. All populations were tested and found to be free from infection with any detectable nepoviruses.

Crossbred larvae, used in some tests, were obtained using the methods described in Chap. IX : 2 : 4 : 2.

X : 2 : 2 Strains of AMV and SLRV

The strains of virus used were: AMV-T (Harrison, 1958); AMV-W (Clark, 1976); SLRV-T (Lister, 1964); SLRV-Ip and SLRV-Ir Italian strains from Prunus persica L. and Rubus idaeus L. (obtained from F. Roca, Bari, Italy). The five strains of virus were propagated in various herbaceous plants at the SCRI. Gel-diffusion serological tests (by A.F. Murant; using antiserum to SLRV-T) showed that SLRV-Ip, SLRV-Ir and SLRV-T differed antigenically. Therefore, SLRV-T, SLRV-Ip and SLRV-Ir were considered to be separate strains of SLRV.

X : 2 : 3 Virus transmission systems

Three wk old seedlings of Chenopodium quinoa Willd. (used for SLRV-T, SLRV-Ip, SLRV-Ir and AMV-W) or Petunia hybrida Vilm. (used for AMV-T) were transplanted into 25 ml plastic pots without drainage holes, manually inoculated with virus and used as sources from which groups of c. 35 virus-free nematodes could acquire virus. The pots were maintained in temperature controlled cabinets (Taylor and Brown,

1974) at 18 C and with supplementary lighting to provide a minimum daylength of 16 hr. After 4 wk access to the virus source plant roots the nematodes were extracted, counted and hand picked individually or in groups of two or five into clean 25 ml plastic pots without drainage holes containing one P. hybrida or three C. quinoa, virus-free, bait plants. After 4 wk access to the bait plant roots the nematodes were extracted and counted.

The root systems of the virus source and bait plants were washed in running tap-water, examined for root galls, which were indicative of nematode feeding activity, and tested for virus by comminuting the roots and rubbing the resultant suspension on to the leaves of C. quinoa indicator plants. In several tests the aerial parts of the bait plants were retained and frozen (-20 C) and those from plants in which virus had been detected in the root systems were subsequently tested for the presence of systemically translocated virus. Virus from some of the C. quinoa assay plants was used in serological tests to confirm the identity of the viruses tested.

In those tests where, for various reasons, these procedures were not strictly adhered to further procedural details are given in the results section e.g. virus source plants originally infected by nematodes.

The percentages of nematodes transmitting virus in each test were calculated using the maximum likelihood estimator of Gibbs and Gower (1960).

X : 2 : 4 Virus transmission from virus source plants infected with virus by nematodes.

X. diversicaudatum from pops. 1, 15 and 17 were used in an experiment to examine their ability to acquire and transmit AMV-T from

plants which previously had been infected with AMV-T by nematodes from the same population. Also, the consecutive transmission of AMV-T to, acquisition from and resultant transmission to, further plants by nematodes from pops. 1, 15 and 17 was examined.

In these studies replicated groups of c. 35 nematodes from each population were given access to manually inoculated virus source plants and, after 4 wk hand-picked groups of 5 nematodes were given access to bait plants using the system described in Chap. X:2:3. Upon completion of the "bait" period the nematodes were extracted, counted and discarded. After the root galls were counted approximately half of each bait plant root system was excised from the bait plant and the bait plants were transferred to clean pots. The excised portion of bait plant root was then tested for the presence of virus using the procedure described in Chap. X:2:3. Those bait plants, in which the excised root systems were found to contain virus, were used as virus source plants in the subsequent test. This procedure was repeated until no virus was detected in any of the bait plants used with nematodes from pops. 15 and 17.

X : 2 : 5 Ingested and retained virus

When root galls are initiated by nematodes feeding on the roots of virus source plants it does not necessarily indicate that the nematodes had access to virus in the plants. The presence of virus in nematodes has been demonstrated by various techniques. Sanger, Allen and Gold (1962) detected tobacco rattle virus in trichodoroid nematodes by inoculating indicator plants with the bodies of comminuted nematodes. A similar "slash test" (Yassin, 1968) was used to detect various nepoviruses in Longidorus vectors. However, the "slash test" technique was not always successful, particularly when Xiphinema spp. and their associated viruses were examined (Taylor and

Murant, 1969; McElroy et al., 1977).

Even when the "slash test" was improved to allow single nematodes to be tested, nepoviruses were not detected in all nematodes containing virus as the number of nematodes that yielded virus in these tests was smaller than the number which transmitted virus (Trudgill and Brown, 1978a).

Immunosorbent electron microscopy (ISEM) is a sensitive serological technique which can be used to detect virus particles in infected plant tissue and even in single aphids containing virus (Robertson and Harrison, 1979). Therefore, this technique was applied to the detection of several nepoviruses in their vector nematodes including AMV-T, SLRV-T, and SLRV-Ip in X. diversicaudatum. The technique proved to be successful, giving reliable results with X. diversicaudatum and its associated viruses. Therefore, ISEM was used to ensure that nematodes used in the virus transmission tests had had access to virus in the virus source plants. It is important to note that ISEM is used to identify virus particles whereas the "slash test" depends on the infectivity of the virus and the reaction in plants to indicate the presence of virus. The ISEM technique, applied to the detection of nepoviruses in their vector nematodes, has been described elsewhere (Robertson and Brown, 1980) therefore it is not repeated here.

Taylor and Robertson (1970) described the site of retention of AMV-T in X. diversicaudatum and using similar techniques Robertson (1975) identified and described the site of retention of SLRV-T in X. diversicaudatum.

In a series of tests headless bodies of nematodes were examined by ISEM. The heads were fixed in 3% glutaraldehyde, postfixed in 1%

osmium tetroxide, sectioned and examined with an electron microscope for virus particles retained within the odontophore, anterior oesophagus and oesophageal bulb (Taylor and Robertson, 1970).

X : 3 RESULTS

X : 3 : 1 Transmission of AMV-T by populations of X. diversicaudatum.

Of the 11 X. diversicaudatum populations tested as vectors of AMV-T, 8 populations appeared to be frequent vectors of the virus (Tab. 44). Pops. 1, 5, 8, 9, 14, 20, 21 and 24 frequently transmitted AMV-T and it was calculated, from the results obtained using groups of 2 nematodes, that about three quarters or more of the individuals in these populations transmitted AMV-T. In contrast to these results it appeared that less than 2 out of 100 individuals from pops. 17 and 23 transmitted AMV-T; pop. 25 from the USA transmitted AMV-T at a rate intermediate between those obtained for the frequent and infrequent virus transmitting populations. From the results obtained, with the groups of two and five nematodes, it was calculated that only about one quarter of the nematodes tested from pop. 25 transmitted AMV-T.

The method of calculating the percentage of nematodes transmitting virus is based on the proportion of bait plants not infected with virus (Gibbs and Gower, 1960). For the populations of X. diversicaudatum which frequently transmitted AMV-T the percentages of nematodes transmitting virus could be accurately determined only from the results of the tests in which groups of two nematodes were used. Because, in these tests with groups of two nematodes less than 100% of the plants became infected with virus whereas in tests with groups of five nematodes generally all the plants became infected.

X : 3 : 2 Transmission of AMV-W by populations of X. diversicaudatum.

AMV-W appeared to be less frequently transmitted than AMV-T by most populations of X. diversicaudatum tested (Tab. 45). It was calculated, when groups of two nematodes from each population were tested, that only about one fifth of the nematodes each from 7 populations transmitted AMV-W. However, about one third of the nematodes from pops. 20 and 21 and conversely only 2% of nematodes from pops. 15 and 17 were calculated to have transmitted AMV-W when groups of two nematodes were tested.

The rates of transmission of AMV-W generally increased when groups of five nematodes were used in the tests. For example, almost one half and one third of the nematodes from pops. 1 and 2 respectively were calculated to transmit AMV-W, when groups of five nematodes were tested. This compared with only one fifth of the nematodes calculated to transmit when groups of two nematodes were tested. But, with pops. 8 and 20 the transmission rates of AMV-W were less when groups of five nematodes were used.

Pops. 15 and 17 appeared to be infrequent vectors of AMV-W independent of the numbers of nematodes used in the tests. And, it was calculated for pop. 23, which did not transmit AMV-W in tests with groups of two and five nematodes, that less than one individual in a hundred may be able to transmit AMV-W.

X : 3 : 3 Factors affecting the transmission of AMV-T.

X : 3 : 3 : 1 Different virus source and bait plants.

In tests, using groups of two X. diversicaudatum, it was calculated that more than 70% of individuals from each of several populations transmitted AMV-T (Tab. 44) but, in similar tests with

AMV-W less than 35% transmitted virus (Tab. 45). Petunia hybrida virus source and bait plants were used in the tests with AMV-T whereas, in the tests with AMV-W Chenopodium quinoa virus source and bait plants were used. What effect, if any, the different virus source and bait plants may have on these rates of transmission was examined in a separate test.

P. hybrida and C. quinoa were examined as virus source and bait plants using groups of two and five X. diversicaudatum from pops. 1, 8 and 9 and AMV-T. Where P. hybrida was used the numbers of transmissions were similar to those obtained in the earlier test with AMV-T in which P. hybrida had also been used (Tabs. 46 and 44). However when C. quinoa was used the rates of transmission showed a decrease compared with the results obtained with P. hybrida. When groups of two X. diversicaudatum from pops. 1, 8 and 9 were used with P. hybrida it was calculated that the mean number of nematodes transmitting virus, from the three populations, was 75% whereas, with C. quinoa the number was only 54%. Therefore, the use of C. quinoa, as the virus source and bait plants, reduced the rate of transmission of AMV-T by 20% when compared with P. hybrida.

If the above result is extrapolated to the results obtained with AMV-W it would seem that AMV-W may be relatively less frequently transmitted than AMV-T by several populations of X. diversicaudatum (Tabs. 45 and 46). But further tests with AMV-T and AMV-W with P. hybrida are required to confirm this result.

X : 3 : 3 : 2 Effect of virus source plants infected with AMV-T which had been transmitted by X.diversicaudatum.

The maintenance of virus cultures by consecutive manual inoculations to host plants has resulted in the apparent loss of transmissibility of isolates of several aphid transmissible viruses

e.g. sugarcane mosaic virus (Koike, 1979). Possible selection by nematodes of transmissible virus, as occurs with some aphid and virus associations, was examined in a series of tests.

The transmission of AMV-T was examined in consecutive tests using groups of five X. diversicaudatum from pops. 1, 15 and 17 and virus source plants which had been infected with virus in each preceding test by nematodes from the respective populations. An initial virus transmission test was begun using virus source plants manually inoculated with AMV-T and nematodes from pops. 1, 15 and 17. The bait plants used in this initial test, upon completion of the test, had half of their root systems removed and checked for the presence of virus. The bait plants, with their remaining root systems, were transplanted into clean pots. Subsequently, those plants which were shown to have virus associated with their root systems were used as virus source plants in test 1, the results of which are given in Tab. 48. This procedure was repeated in this series of consecutive virus transmission tests and full procedural details are given in Chap. X:2:4.

The results obtained in this series of consecutive virus transmission tests are similar to the results obtained in earlier tests (Tabs. 44, 47 and 48). Nematodes from pop. 1 frequently transmitted AMV-T whereas nematodes from pops. 15 and 17 only infrequently transmitted AMV-T. The use of virus source plants which had been naturally infected with AMV-T by nematodes from a given population did not affect the frequency of transmission of virus by the nematodes from the same population.

In a separate test an isolate of AMV-T (AMV-Tn) was used which had been recovered from the roots of a bait plant to which two X. diversicaudatum from pop. 17 (Italian) had been given access in an

earlier test (Chap. X:3:1). AMV-Tn was manually inoculated to a series of P. hybrida virus source plants to which X. diversicaudatum from pops. 1, 15 and 17 were given access and a virus transmission test was carried out using the procedures described in Chap. X:2:3.

The results from this test were similar to results obtained in an earlier test which used an isolate of AMV-T which had been maintained in plant hosts by a succession of manual passages over several years (Tabs. 44 and 47). The nematodes from pop. 1 readily transmitted AMV-Tn whereas few nematodes from pop. 17 transmitted the virus. Nematodes from pop. 15, from France, transmitted AMV-Tn at a rate intermediate between those obtained with pops. 1 and 17 (Tab. 47). Therefore, an isolate of AMV-T maintained for several years as a laboratory culture and an isolate, transmitted by X. diversicaudatum, newly obtained from a bait plant behaved similarly in separate virus transmission tests. No differences were detected in their relative frequencies of transmission by populations of X. diversicaudatum.

X : 3 : 4 Transmission of SLRV-T by populations of X. diversicaudatum.

In tests with groups of two and five nematodes 8 of 11 populations of X. diversicaudatum relatively frequently transmitted SLRV-T. It was calculated that about one third of the nematodes from these populations transmitted virus in the study. With these 8 populations the percentages of nematodes transmitting virus in the tests with groups of two and five nematodes were relatively similar. But, in tests with groups of two nematodes it was calculated that 65% and 23% of nematodes in pops. 9 and 21 respectively transmitted virus. Whereas, with groups of five nematodes 32% and 37% of the nematodes from pops. 9 and 21 respectively transmitted virus. These results require further investigation as similiar differences were

recorded with AMV-W and populations of X. diversicaudatum (Chap. X : 3 : 2).

Pop. 25, from the USA, was a less frequent vector of SLRV-T than pops. 1, 5, 8, 9, 14, 20, 21 and 24 and it was calculated that only about one fifth of the nematodes from this population transmitted virus. Nematodes from pops. 17 and 23 only infrequently transmitted SLRV-T but rather more nematodes from pop. 23 than from pop. 17 were calculated to have transmitted virus (Tab. 49).

X : 3 : 5 Transmission of SLRV-Ip by populations of X. diversicaudatum.

SLRV-Ip and pop. 17 were both originally obtained from northern Italy but were not found occurring together. However, pop. 17 only infrequently transmitted SLRV-Ip and it was calculated that less than 3% of the nematodes used in tests with groups of two and five nematodes transmitted the virus (Tab. 50). Also, one group of five nematodes from pops. 9 and 23 and one group of two nematodes from pop. 25 but none of the other seven populations transmitted the virus (Tab. 50). Therefore, in the present study SLRV-Ip was most frequently, and consistently, transmitted by pop. 17.

X : 3 : 6 Effect of different bait plants on the transmission of three strains of SLRV.

The effect of different bait plants on the transmission of SLRV-T, SLRV-Ip and SLRV-Ir by groups of five nematodes from pop. 1 was examined in a separate study. The nematodes were allowed access to virus infected C. quinoa virus source plants and then groups of five nematodes were given access to C. quinoa, Gomphrena globosa L., Rubus ideaus L. and Fragaria x ananassa Duch. bait plants using the procedure described in Chap. X:2:3.

SLRV-Ip and SLRV-Ir were not transmitted to any of the bait plants used in the study which confirmed earlier results obtained with SLRV-Ip and nematodes from pop. 1 (Tabs. 50 and 51). Nematodes from pop. 1 transmitted SLRV-T to all of the C. quinoa bait plants, but to only 8 of 10 G. globosa and to 1 of 10 of the R. ideaus and of F. x ananassa bait plants. Therefore, of the bait plants used in the study, C. quinoa appeared to be most suited for studying the transmission of SLRV-T by nematodes from pop. 1. Also, the results obtained with the other bait plants species and SLRV-T demonstrated that, as with AMV-T (Chap. X:3:3:1), the choice of bait plant may markedly affect the results obtained in the tests examining the transmission of the virus by nematodes.

X : 3 : 7 Transmission by three populations of X. diversicaudatum, of isolates of SLRV-T, SLRV-Ip and SLRV-Ir which had previously been transmitted by X. diversicaudatum from Italy.

As had previously been examined with AMV, the effect on the subsequent rates of transmission by nematodes of using isolates of SLRV which previously had been transmitted by nematodes was examined. Isolates of SLRV were chosen which had been recovered from the roots of C. quinoa bait plants to which X. diversicaudatum from pop. 17 had been given access (SLRV-Tn, SLRV-Ipn and SLRV-Irn). The nematode-transmitted isolates of SLRV were manually inoculated to a series of C. quinoa virus source plants to which X. diversicaudatum from pops. 1, 15 and 17 were given access and a virus transmission test was carried out using the procedures described in Chap. X:2:3.

The results obtained were similar to results obtained in earlier tests in which isolates of SLRV used had been maintained in plant hosts in the laboratory by a succesion of manual passages over several

years (Tabs. 52, 50 and 49). Nematodes from pop. 1 relatively frequently transmitted SLRV-Tn but did not transmit SLRV-Ipn or SLRV-Irn. Nematodes from pop. 15 did not transmit SLRV-Ipn and only infrequently transmitted SLRV-Tn but nematodes from pop. 17 infrequently transmitted all three viruses. Therefore, as had previously been found with AMV, laboratory-maintained isolates of SLRV as well as those recently transmitted by nematodes behave similarly in virus transmission studies and both types of isolate are transmitted with the same relative frequencies.

X : 3 : 8 Ingested and retained virus.

The availability, to X. diversicaudatum, of AMV-T, SLRV-T and SLRV-Ip in virus source plants was examined by using ISEM. Also, the retention of the viruses in the nematodes oesophagi was examined with the aid of an electron microscope.

Individual nematodes from pops. 1, 15 and 17 were collected from virus source plants from virus transmission tests with AMV-T, SLRV-T and SLRV-Ip (Tabs. 44, 49 and 50). The anterior region, containing the oesophagus, of each nematode was removed and the remaining body was processed and examined for the presence of virus particles by using ISEM. Meanwhile the anterior region of each nematode was processed and thin sections were taken and examined for the presence of virus particles.

The results of the ISEM study showed that all the nematodes examined had ingested virus (Tab. 53). Therefore, the viruses SLRV-T, SLRV-Ip and AMV-T in the virus source plants apparently had been available to the nematodes. The low rates of transmission of these viruses, by different populations, therefore, cannot be attributed to the lack of availability of these viruses to the nematodes used in the tests.

The examination of the nematodes' anterior regions for the presence of virus particles revealed that, in general, virus was associated with nematodes where large frequencies of transmission had occurred e.g. AMV-T and SLRV-T with nematodes from pop. 1 (Tab. 54). However, SLRV-T particles were also observed in one of the three nematodes examined from pop. 15. Therefore, small frequencies or no transmission of virus by X. diversicaudatum populations, used in the study, may have been the result of a general lack of retention of the virus within the nematodes.

X : 3 : 9 Transmission of viruses by X. diversicaudatum produced from Scottish and Italian parental lines and as reciprocal crossbred lines.

The nematodes used in this study were obtained by using the culturing technique described in Chap. IX:2:4:2. Four lines of progeny were produced:- Scottish maternal and paternal parentage (SS progeny); Italian maternal and paternal parentage (II progeny); Scottish maternal and Italian paternal parentage (SI progeny) and Italian maternal and Scottish paternal parentage (IS progeny). These four lines are referred to as the F1 progeny in the study and progeny produced by F1 nematodes are referred to as F2 progeny.

The virus transmission test system described in Chap. X:3:2 was used for the study but only one nematode was used with each bait plant.

AMV-T was transmitted by c. 80% of the SS nematodes but by only 4% of the II nematodes. This result was similar to those obtained in earlier tests using nematodes from the Scottish and Italian populations (Tabs. 44, 47 and 48). However, the hybrid nematodes transmitted AMV-T with frequencies intermediate to those of the parent

populations. Also, the SI F1 and F2 nematodes transmitted AMV-T almost twice as frequently as the IS F1 and F2 nematodes and both F2 crosses transmitted AMV-T more frequently than the F1 crosses.

The transmission of SLRV-T by the II nematodes was similar to results obtained in earlier tests but, the SS nematodes transmitted SLRV-T more frequently than did Scottish nematodes in these earlier tests (Tabs. 56, 49, 51 and 52). The hybrid nematodes transmitted SLRV-T with frequencies intermediate to those of the parent populations which was similar to the result obtained with AMV-T. However, SLRV-T was transmitted more frequently by the IS nematodes than by the SI nematodes which was the converse of the result obtained with AMV-T. As with AMV-T, the SI and IS F2 nematodes transmitted SLRV-T more frequently than the SI and IS F1 nematodes.

One of 30 II and two of 30 IS F2 nematodes transmitted SLRV-Ip but none of the SS, SI F1, IS F1 and the SI F2 nematodes transmitted the virus (Tab. 57).

X : 4 DISCUSSION

Results from the present study support previously unsubstantiated reports by Dalmasso et al. (1972) and Martelli (1975, 1978) that differences exist in the relative abilities of populations of X. diversicaudatum to transmit AMV-T. Furthermore these differences were found with AMV-W, SLRV-T and SLRV-Ip. Also the differences could be used to classify the X. diversicaudatum populations into groups e.g. with AMV-T pops. 1, 5, 8, 9, 14, 20, 21 and 24 could be cosidered good or efficient virus vector populations; pop. 25 which was less efficient, a moderate virus vector population and pops. 15, 17 and 23 which transmitted AMV-T only infrequently were poor virus vector populations. Choice of virus or virus strain altered the composition of the groups but overall nematodes from pops. 15, 17 and

23, from southwest Europe, were poor virus vectors whereas nematodes from all other populations examined were moderate to good virus vectors.

The isolates of AMV-T, AMV-W, SLRV-T and SLRV-Ip used in the studies reported here, were obtained from cultures maintained in the glasshouse, for several years, by consecutive manual inoculations to host plants. This method of maintaining virus cultures has resulted in the apparent loss of transmissibility of some isolates of some aphid transmissible viruses (Koike, 1979). Therefore, isolates of AMV-T, SLRV-T, SLRV-Ip and SLRV-Ir which had been transmitted to bait plants, by X. diversicaudatum from Italy, were transferred by manual inoculation to a series of virus source plants. Nematodes from pops. 1, 15 and 17 were used to transmit these isolates and the results obtained were similar to those obtained in earlier tests. Also, nematodes from pops. 1, 15 and 17 were used to transmit AMV-T from plants previously infected with virus by nematodes from these same populations. This procedure was repeated in consecutive tests but no differences were found in the transmissibility of the virus. Therefore it appears unlikely that the original isolates of AMV-T, SLRV-T, SLRV-Ip and SLRV-Ir used in the series of tests, had been affected in their transmissibility by nematodes or by their method of culturing, unlike some aphid transmitted viruses (Koike, 1979).

Further studies were done to try to explain the apparent differences which existed in the relative abilities of X. diversicaudatum populations to transmit viruses. Petunia hybrida virus source and bait plants had been used in the studies with AMV-T but C. quinoa plants had been used in the studies with AMV-W, SLRV-T and SLRV-Ip. An experiment in which these two plant species were compared as virus source and bait plants, with AMV-T and three

populations of X. diversicaudatum, revealed that the choice of plant species could substantially affect the frequency of virus transmission by the nematodes. Approximately one fifth more X. diversicaudatum transmitted AMV-T when the P. hybrida plants were used than when C. quinoa plants were used. This result, extrapolated to the other studies, revealed the presence of relative differences in the frequencies with which the different viruses were transmitted under standard conditions by a given population of X. diversicaudatum. Excluding the results obtained with pops. 15, 17 and 23 with AMV-T, AMV-W and SLRV-T, and using only the results from groups of two nematodes, the average percentages of nematodes, from the remaining populations, transmitting these viruses were c. 72% for AMV-T, c. 30% (c. 25% plus one fifth for the extrapolated correction factor) for AMV-W and c. 42% (c. 35% plus one fifth) for SLRV-T. Therefore, differences exist between populations of X. diversicaudatum in their abilities to transmit a given virus; and differences exist in the frequencies of transmission of different viruses by a given population of X. diversicaudatum.

The choice of P. hybrida and C. quinoa as virus source plants appeared to be satisfactory in tests with SLRV-Ip as nematodes from three X. diversicaudatum populations tested, by ISEM, were found to have had access to and to have ingested virus from the virus source plants. Root galls, caused by nematodes' feeding, were found on the roots of the bait plants which indicated that the nematodes in all the studies, had had the opportunity to transmit any virus which they were carrying.

Taylor and Robertson (1970) and Robertson (1975) reported the presence of specific sites of retention of AMV-T and SLRV-T in X. diversicaudatum. These sites of retention were examined in a few

X. diversicaudatum from pops. 1, 15 and 17 which had been given access to AMV-T, SLRV-T and SLRV-Ip. In general, virus particles were present in those nematode - virus combinations where the virus had been relatively frequently transmitted. Therefore, it is probable that lack of virus transmission resulted from an inability by X. diversicaudatum to specifically retain virus and not the result of the nematodes inability to release virus retained at specific sites of virus retention, as is reported to happen with L. macrosoma and raspberry ringspot viruses (Harrison, Robertson and Taylor, 1974; Trudgill and Brown, 1978b).

A further series of tests demonstrated that the ability of X. diversicaudatum to transmit AMV and SLRV was hereditary. In these tests AMV-T, SLRV-T and SLRV-Ip were used with F1 hybrid X. diversicaudatum crossbred from Scottish and Italian parental lines and F2 hybrids bred from the F1 hybrids. The choice of maternal and paternal lines affected the resultant hybrids abilities to transmit the viruses. With AMV-T and SLRV-T the F1 hybrids, bred from Italian maternal and Scottish paternal lines (IS F1) gave similar results when transmitting the viruses as did the subsequent F2 hybrids (IS F2). From the results with the IS F1 and IS F2 nematodes it may be speculated that the ability of these nematodes to transmit virus showed genetic incomplete dominance. But, with AMV-T and Scottish maternal and Italian paternal F1 hybrids (SI F1) and the subsequent F2 hybrids (SI F2) the hybrid nematodes abilities to transmit virus shows no genetic dominance effects. With SLRV-T and SI F1 and SI F2 hybrids transmission of the virus may be attributed to genetic complete dominance. Little is known about the genetics of virus transmission by longidoroid nematodes. Therefore it is not possible to refer to dominance effects until it is known if one or several genes are responsible for the ability of these nematodes to transmit

viruses. The present tests with hybrid nematodes demonstrate that the ability of X. diversicaudatum to transmit viruses is hereditary; the potency of the hybrid nematodes as virus vectors is affected by maternal and paternal lines and the genetic influence on hybrids possibly is contained in extranuclear elements rather than in the cytoplasm during fertilization. Furthermore, the hereditary nature of the nematodes ability to transmit viruses involves the nematodes ability to specifically retain virus particles in its feeding apparatus.

How viruses are adsorbed to the cuticular lining of the virus vector nematodes oesophagus remains a matter for speculation. Harrison et al. (1974) reported that the protein coat of virus particles was important in the specific transmission of a virus by its nematode vector. Furthermore it has been suggested that the surface charge density on the protein coat of virus particles may be a factor in the association and that the nature of the cuticle providing the site of retention in the odontophore and oesophagus may, in part, be involved (Taylor and Robertson, 1977; Taylor and Brown, 1981). Robertson and Wyss (1983) report that the food canal in X. index, the area where virus is specifically retained, can be stained for carbohydrates and because sialic acid plays an important role at virus receptor sites on membranes (Leanloz and Codlington, 1976) this substance may be involved in the specific retention of viruses in virus vector nematodes. It is further speculated by Robertson and Wyss (1983) that gangliosides (charged glycolipids) may be involved by providing binding sites for the specific adsorption of viruses within nematodes. Alternatively, it has been suggested by several research groups that "mucus-like" material may be involved in the specific retention of viruses within virus vector nematodes and such a substance has been observed associated with virus at specific sites of

virus retention in three virus vector genera Longidorus, Xiphinema and Paratrichodorus (Taylor and Robertson, 1969, 1970; McGuire, Kim and Douthit, 1970; Robertson and Wyss, 1983).

It is possible that any of the above methods either individually or in different combinations, or even as yet undiscovered methods, may be responsible for the specific adsorption of viruses within virus vector nematodes. Furthermore, different methods of adsorption may be found in different nematode genera and with serologically different viruses vectored by the same nematode species.

Differences in the frequency of transmission between viruses and virus strains by nematodes may be related to the nature and strength of the bond between the virus and the virus receptor sites within the nematode. Also differences in virus transmission may be related to a secondary form of virus retention within the vector nematode - virus to virus attachment (Robertson and Wyss, 1983). After the primary (initial) attachment of virus particles, as a monolayer, at virus receptor sites second and even subsequent layers of particles may become attached to the primary monolayer. The ability of a nematode to transmit virus is dependent on the primary attachment of virus particles to the receptor sites within the nematode. The resultant frequency of transmission and the persistence of transmissible virus within the nematode is dependent on the strength of the force between particle and receptor site. Also, the secondary form of attachment taken together with the primary attachment may influence the frequency of transmission and persistence of virus within the nematode. Differences in the frequencies of transmission between the different viruses and virus strains used with populations of X. diversicaudatum suggest that the nature of the forces acting on the primary and/ or secondary forms of attachment were different. Therefore it is likely

that the nature of the specificity between SLRV-Ip, SLRV-T and AMV-T with X. diversicaudatum are different. This suggestion is further supported by the basic inherent differences in the transmission of these viruses by hybrid F1 and F2 X. diversicaudatum.

Harrison, Mowat and Taylor (1961) were the first to suggest that serologically distinctive forms of nepoviruses had different specific nematode vectors e.g. L. elongatus was the vector of the type strain of tomato blackring virus (TBRV) and L. attenuatus was the vector of a serologically different strain of TBRV. Brown and Taylor (1981) further suggested that the degree of specificity may differ between populations of a nematode vector species e.g. three geographically separated isolates of TBRV and three strains of raspberry ringspot virus were transmitted more frequently by a population of L. elongatus from Scotland than from England. The results obtained in the present study support and extend the suggestion that serologically distinctive strains of nepoviruses have specific nematode vectors. Differences have been shown to exist between populations of X. diversicaudatum and their respective abilities to transmit individual viruses and virus strains. Furthermore, differences have been shown to exist in the frequencies of transmission of serologically distinctive viruses and strains of a virus by individual populations of X. diversicaudatum. Therefore, for Xiphinema species which are able to transmit virus, the nature of specificity between nematode species and viruses may differ and perhaps the specificity also differs between populations of the same nematode and strains of the same virus.

Much variability was present in the abilities of different X. diversicaudatum populations to transmit viruses and virus strains. This variability may be used to erect several different groupings of populations but, overall, only two groups of populations appear to

exist viz., those populations which are generally effective at transmitting viruses and those populations from southwest Europe, which apparently are relatively ineffective at transmitting viruses. The viruses could also be placed into two groups viz., AMV-T, AMV-W and SLRV-T all of which were readily transmitted and a second group containing SLRV-Ip and SLRV-Ir which were transmitted consistently only by the nematodes from an Italian population although at a small rate. Although specific relationships such as these exist between viruses and their vector nematodes little is known about the effects of these organisms on one another; X. index survival during starvation was significantly better for those nematodes which had been given access to viruliferous hosts than for nematodes given access to virus-free hosts prior to the experiment (Das and Raski, 1969); while Roggen (1966) suggested that grapevine fanleaf virus acquired by X. index may affect the nematodes osmoregulation, cause an increase in the size of nuclei in the lateral chords, an enlargement of the pseudocoelomic cavity and could have been responsible for an increase in the amount of RNA present in the nematodes. X. index appears to have an effect on the virus which it specifically retains: for example, grapevine fanleaf virus (GFLV) in X. index can persist and subsequently be transmitted eight months after the nematode aquires the virus whereas, in vitro GFLV in Chenopodium sap at 18-20 C remains infective only for 10-28 days (Taylor, 1971). The techniques and methods used in the present study to examine the transmission of virus and the reproductive biology of X. diversicaudatum may be used further to examine the effects on each other of virus and vector nematode. Also these techniques may be used to identify plants, especially crop species, resistant and tolerant to both virus and vector nematode.

X : 5 CONCLUSIONS

1) Arabis mosaic (AMV) and strawberry latent ringspot (SLRV)

viruses and serologically distinguishable strains of these viruses are transmitted with different efficiencies by their nematode vector, X. diversicaudatum.

2) Populations of X. diversicaudatum differ in their abilities to transmit AMV and SLRV and serologically distinguishable strains of these viruses. In laboratory tests populations of the nematode from southwest Europe infrequently transmitted the viruses compared with populations from other parts of Europe, New Zealand and the USA.

3) In experiments using standardised techniques to examine transmission of viruses by nematodes the choice of plant species used as the virus source and as bait plants can affect the frequency of transmission by the nematodes. In tests with X. diversicaudatum and AMV the relative frequency of virus transmission by nemtodes was 20% more with P. hybrida than with C. quinoa virus source and bait plants.

4) A strain of SLRV from northern Italy was consistently only transmitted by a population of X. diversicaudatum from the same geographical area but with a relatively small efficiency. Populations of the nematode from other areas of Europe, New Zealand and the USA rarely and inconsistently transmitted this virus.

5) The lack of transmission of the Italian strain of SLRV by populations of X. diversicaudatum and the relatively small rates of transmission of serologically distinguishable strains of SLRV and AMV by nematodes from southwestern Europe were due to a lack of specific retention of these viruses by the nematodes.

6) The ability to transmit serologically distinguishable strains of AMV and SLRV is hereditary involving adsorption of virus particles at specific sites within the nematode. Furthermore, it seems that the nature of the nematode/virus specificity differs for AMV-T, SLRV-T and SLRV-Ip and that maternal and paternal parents influence the frequency of transmission of the viruses by the hybrid nematodes.

TABLE 44 : Transmission of AMV-T by groups of two and five *X. diversicaudatum* from 11 populations.

Population*	Numbers of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
1	23/25**	12/12**	72	more than 39
5	24/25	12/12	80	more than 39
8	24/25	12/12	80	more than 39
9	23/25	12/12	72	more than 39
14	25/25	12/12	more than 80	more than 39
17	1/35	0/15	1.4	less than 1.4
20	24/25	12/12	80	more than 39
21	24/25	12/12	80	more than 39
23	0/20	1/15	less than 2.5	1.4
24	24/25	12/12	80	more than 39
25	12/25	9/12	28	24

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 45 : Transmission of AMV-W by groups of two and five *X. diversicaudatum* from 12 populations.

Population*	Numbers of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
1	9/25**	14/15**	20	42
5	9/25	13/15	20	33
8	9/25	4/7	20	16
9	10/25	12/15	23	28
14	9/24	na***	18	na
15	1/25	0/6	2	less than 3.6
17	1/25	0/10	2	less than 1.4
20	15/25	4/10	37	9.7
21	13/25	6/7	31	32
23	0/20	0/15	less than 2.5	less than 1.4
24	10/25	8/10	23	28
25	9/25	7/9	20	26

*, For explanation of codes see Table 31.
**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.
***, Not available.

TABLE 46: Effect of different virus source and bait plants on the transmission of AMV-T by groups of two and five X. diversicaudatum from three populations.

Population*	Numbers of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
		Petunia hybrida		
1	23/25**	12/12	72	more than 39
8	24/25	12/12	80	more than 39
9	23/25	12/12	72	more than 39
		Chenopodium quinoa		
1	19/25	14/15	51	42
8	21/25	12/12	60	more than 39
9	19/25	14/15	51	42

*, For explanation of codes see Table 31.
**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 47 : Transmission of an isolate of AMV-T by groups of two and five *X. diversicaudatum* from three populations.

Population*	Numbers of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
1	18/20**	12/12	68	more than 39
17	1/22	0/15	2.3	less than 1.4
15	10/40	0/6	13	less than 3.6

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 48 : Transmission of AMV-T in consecutive tests with groups of five X. diversicaudatum from three populations and virus source plants which had been infected with virus in each preceding test by nematodes from the respective populations.

Population*	Test							
	1		2		3		4	
1	20/20**	>45***	14/15	42	13/13	>40	15/15	>42
15	3/20	3.2	3/22	2.9	2/18	2.3	0/12	<1.7
17	2/20	2.1	0/15	<1.4	na		na	

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

***, Calculated percentages of nematodes transmitting virus.

na, Not available.

Table 49 : Transmission of SLRV-T by groups of two and five X. diversicaudatum from 11 populations.

Population*	Numbers of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
1	16/31**	15/16	30	43
5	16/25	9/10	40	37
8	15/25	9/10	37	37
9	22/25	6/7	65	32
14	12/25	4/5	28	28
17	1/35	0/15	1.4	less than 1.4
20	15/25	6/6	37	more than 30
21	10/25	9/10	23	37
23	3/20	2/10	7.8	4.4
24	14/25	8/10	34	28
25	9/25	6/9	20	20

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 50 : Transmission of SLRV-Ip by groups of two and five *X. diversicaudatum* from 11 populations.

Populations*	Number of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
1	0/40**	0/20	less than 1.3	less than 1
5	0/25	0/10	less than 2	less than 2.1
8	0/25	0/10	less than 2	less than 2.1
9	0/24	1/10	less than 2.1	2.1
14	0/19	0/4	less than 2.7	less than 5.6
17	2/35	2/16	2.9	2.6
20	0/22	0/10	less than 2.3	less than 2.1
21	0/24	0/8	less than 2.1	less than 2.6
23	0/20	1/10	less than 2.5	2.1
24	0/20	0/9	less than 2.5	less than 2.3
25	1/23	0/10	2.2	less than 2.1

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 51 : Transmission of three strains of SLRV by X. diversicaudatum from a Scottish population, using Chenopodium quinoa virus source plants and C. quinoa, Gomphrena globosa, Rubus ideaus and Fragaria x ananassa bait plants.

Virus	Bait plant	Number of transmissions*	Calculated percentages of nematodes transmitting virus
SLRV-T	C. quinoa	10/10**	more than 37
	G. globosa	8/10	28
	R. ideaus	1/10	2.1
	F.x ananassa	1/10	2.1
SLRV-Ip	C. quinoa	0/10	less than 2.1
	G. globosa	0/10	less than 2.1
	R. ideaus	0/10	less than 2.1
	F.x ananassa	0/10	less than 2.1
SLRV-Ir	C. quinoa	0/10	less than 2.1
	G. globosa	0/10	less than 2.1
	R. ideaus	0/10	less than 2.1
	F.x ananassa	0/10	less than 2.1

*, Groups of five nematodes per bait plant.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 52 : Transmission of isolates of SLRV-T, SLRV-Ip and SLRV-Ir by groups of two and five X. diversicaudatum from three populations.

Population*	Number of nematodes per replicate			
	2	5	2	5
	number of transmissions		calculated percentages of nematodes transmitting virus	
		SLRV-T		
1	17/25**	12/12	43	more than 39
15	4/40	1/4	5.1	5.6
17	0/24	3/15	less than 2.1	4.4
		SLRV-Ip		
1	0/25	0/20	less than 2	less than 1
15	0/40	0/3	less than 1.3	less than 7.8
17	2/25	1/14	4.1	1.5
		SLRV-Ir		
1	0/25	0/20	less than 2	less than 1
17	2/25	1/12	4.1	1.7

*, For explanation of codes see Table 31.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 53 : Detection of viruses, by immunosorbent electron microscopy (ISEM), in three populations of X. diversicaudatum

Virus	Population*	Replicates in which virus was detected by ISEM
AMV-T	1	4/4**
	15	4/4
	17	4/4
SLRV-T	1	4/4
	15	4/4
	17	4/4
SLRV-Ip	1	4/4
	15	4/4
	17	4/4
Control	1	0/4
(No virus)	15	0/4
	17	0/4

*, For explantion of codes see Table 31.

**, Denominator is number of replicates, numerator is number of replicates in which virus was detected by ISEM.

TABLE 54 : Detection, by electron microscopy, of virus particles in the feeding apparatus of X. diversicaudatum from three populations.

Virus	Population*	Number of nematodes with virus particles associated with their feeding apparatus
AMV-T	1	1/2**
	15	0/2
	17	0/3
SLRV-T	1	2/4
	15	1/3
	17	0/4
SLRV-Ip	1	0/4
	15	0/4
	17	0/4
Control	1	0/4
(No virus)	15	0/4
	17	0/4

*, For explanation of codes see Table 31.

**, Denominator is number of nematodes examined, numerator is number of nematodes in which virus was identified.

TABLE 55 : Transmission of AMV-T by F1 and F2 X. diversicaudatum hybrids produced from Scottish and Italian parental lines.

F1 parental and F2 grandparental lines		Number of transmissions*		Percentage of nematodes transmitting virus	
Female	Male	F1	F2	F1	F2
Scotland	Scotland	67/84**	-	80	-
Italy	Italy	2/49	-	4	-
Scotland	Italy	9/25	16/29	36	55
Italy	Scotland	4/25	9/30	16	30

*, One nematode per bait plant.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 56 : Transmission of SLRV-T by F1 and F2 X. diversicaudatum hybrids produced from Scottish and Italian parental lines.

F1 parental and F2 grandparental lines		Number of transmissions*		Percentage of nematodes transmitting virus	
Female	Male	F1	F2	F1	F2
Scotland	Scotland	54/77**	-	70	-
Italy	Italy	1/57	-	2	-
Scotland	Italy	0/21	4/27	less than 4.8	15
Italy	Scotland	5/23	9/30	22	30

*, One nematode per bait plant.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

TABLE 57 : Transmission of SLRV-Ip by F1 and F2 X. diversicaudatum hybrids produced from Scottish and Italian parental lines.

F1 parental and F2 grandparental lines		Number of transmisions*		Percentage of nematodes transmitting virus	
Female	Male	F1	F2	F1	F2
Scotland	Scotland	0/54**	-	less than 1.9	-
Italy	Italy	1/57	-	2	-
Scotland	Italy	0/11	0/30	less than 9.1	less than 3.3
Italy	Scotland	0/23	2/30	less than 4.3	6.7

*, One nematode per bait plant.

**, Denominator is number of bait plants, numerator is number of bait plants from which virus was recovered.

PART FIVE

"APERCU"

CHAPTER XI

GENERAL DISCUSSION ON SPECIATION IN THE LONGIDOROIDEA

Less than 10% of the current species which comprise the Longidoroidea were described prior to the discovery by Hewitt et al. (1958) that X. index was a vector of grapevine fanleaf virus in vineyards in California, USA. Interest subsequently increased in the taxonomy, biology, ecology, virus transmission and control of longidoroids. The present study was undertaken to identify the presence and distribution of longidoroids in Europe and to examine intraspecific variability present within a longidoroid species. X. diversicaudatum, an amphimictic virus vector species, was chosen as a model for the latter part of the study.

An examination of the many published reports of the occurrence and distribution of longidoroid nematodes in Europe has revealed that 58 species of the Longidoroidea have been recorded from European countries. Furthermore, it has been found that several of these species are widespread in Europe but that many of the species have restricted or localised distributions within only a relatively few European countries. Most species appear to have distinct geographical distributions within Europe and these data combined with data of the species general anatomy and morphology permit groups of species to be formed, each of which, generally, is comprised of an amphimictic (ancestral) and several thelytokous (clonal) species. Also, in general these groups of species agree with the model for evolution in the Longidoroidea proposed by Dalmasso and Berge (1983). Alternative groups of species in the Longidoroidea have been proposed by other workers e.g. Cohn and Sher (1972) split the Xiphinema genus into eight sub-genera based on differences between species in the female reproductive tracts and tail shape. Subsequently, Luc and Dalmasso (1975) rejected this splitting of the genus because the characters

used to distinguish the sub-genera had independent evolutions; thus one could not be proven to take precedence over the other. Robertson and Taylor° (1975) reported that the arrangement of odontostyle retractor muscles could be used to form three groups of Longidorus species and that one of these muscle arrangements was similar to that found in Xiphinema species. The composition of these groups of species does not agree with the groups proposed in the present study, but it is possible that the muscle arrangements are more primitive than the morphological characters used in the present study. However, much research is required to substantiate the groups of species, proposed in the present study, as classical evolutionary groups to which the taxonomic term "sub-generic" might be applied. Therefore, the groups of Longidorus and Xiphinema species proposed in the present study are considered to be artificial, and although useful in the taxonomy of the genera should NOT be considered as sub-genera.

Much variability was found between published reports of morphometrics of different populations of X. diversicaudatum. Part of the present study revealed that these differences may in part have been the result of inherent differences in the microscope systems used to obtain the morphometrics, the influence of the person obtaining the measurements or the method used to process the nematodes for microscopy. The last named, particularly the fixative used and whether or not the nematodes were subsequently processed to glycerol after being fixed, was the cause of significant differences to all of the morphometrics recorded during the study. Therefore, differences in published morphometrics of populations of X. diversicaudatum could be attributed to artifacts of the methods employed to obtain the measurements.

The aforementioned artifacts were reduced to a minimum by

employing a standard system when examining the morphometrics of specimens from several geographically isolated populations of X. diversicaudatum. Much significant variability was found to occur in the morphometrics of the different populations but specimens from all of the populations, although morphologically different, were found to be anatomically similar. Some of the morphometrical differences were used to erect morphometrically most similar groups of populations of X. diversicaudatum. The populations, which anatomically all comprised one species, were found to be morphometrically homogeneous at a level of 80% similarity but at higher levels of similarity the populations began to form discrete groups. Luc and Southey (1980) found that populations of the thelytokous X. elongatum, X. insigne and X. savanicola separated into their species at a level of 75% similarity using the same morphometric characters used in the present study. Therefore, by employing these same morphometric characters it appears likely that numerical taxonomy using canonical variate analysis may be used to help identify species if levels of similarity of less than 80% are used. Morphometric characters different to those used here also may allow numerical taxonomy techniques to be used to help identify species, perhaps even at levels of similarity greater than 80%.

The ratio of males to females was found to vary between populations of X. diversicaudatum. Also, the main reproductive ability of specimens from X. diversicaudatum populations was found to vary between populations and when specimens from the populations were mated with specimens from a Scottish population. The variability in the sex ratios or reproductive abilities of the populations was not related to the morphometrics of the populations. Similarly, variability in the abilities of populations to transmit viruses were not related to the morphometrics of the populations.

The study of virus transmission by populations of X. diversicaudatum revealed that the efficiency of transmission of virus strains by a population varied and that populations transmitted a virus strain with differing efficiencies. Each virus strain generally appeared to be transmitted with a different efficiency by the X. diversicaudatum populations and the transmission of a virus appeared to be a specific relationship between the virus strain and the nematode population. The apparent ability or inability of a nematode population to transmit a virus strain could not exclusively be used to determine the speciation of the population because some populations of a species e.g. X. diversicaudatum may appear unable to transmit a virus strain, whereas other populations of this species are able to do so. It was also found that the ability of a nematode to specifically retain and then transmit a virus was inherited and that the potency of the hybrid nematodes as virus vectors was affected by maternal and paternal lines. Furthermore, the results from this study indicate that the nature of the specificity between AMV-T, SLRV-T and SLRV-Ip with X. diversicaudatum is different.

The morphological species concept which is derived from the typological species concept, based on the philosophies of Plato and Aristotle, is currently used for the taxonomy and systematics of the Longidoroidea. Mayr (1970) defined the morphological species concept, which gives rise to the terminology "morpho-species", as being "Natural populations considered by general consent to be species are morphologically distinct. Morphological distinctness is thus the decisive criterion of species rank. Consequently, any natural population that is morphologically distinct must be recognised as a separate species". Much more widely used in general taxonomy and systematics is the biological species concept, which is based on the

genetic processes inherent in biological organisms. The definition of the biological species concept given by Mayr (1970) states "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups".

Many species in the Longidoroidea are thelytokous but several are amphimictic. If the morphological species concept is applied to the amphimictic species in the Longidoroidea two problems are encountered viz. intraspecific morphological variation which may give rise to speciation and lack of morphological variation which may result in sibling species (populations morphologically similar but reproductively isolated). The biological species concept cannot be applied to the thelytokous species as the individuals in such species are reproductively isolated. Luc and Southey (1980) gave an exposition on the rationale of accepting a definition of species, which encompassed thelytokous forms, proposed by Cronquist (1978) who stated that "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means". However, as recognised by Luc and Southey (1980), this definition of species requires much qualification and must necessarily leave the referral of nematodes to specific rank as subjective, rather than objective, for the taxonomist.

As suggested by Luc and Southey (1980) thelytokous species in the Longidoroidea will remain morpho-species perhaps until such time as techniques are developed to examine and compare the protein composition as influenced by genetic processes, of these nematodes. This may eventually lead to a protein-species classification system being used in the taxonomy of thelytokous Longidoroidea which will be comparable to the biological species concept. However, amphimictic species can be described within the biological species concept by

employing some of the methods described during this study. Therefore, it seems inappropriate to use Cronquist's (1978) single, general definition of a species for the Longidoroidea as two separate species concepts may be used, each of which is currently used in general taxonomy and systematics. Also the concepts are mutually exclusive, each only applicable to those groups of species to which it applies.

X. diversicaudatum is an amphimictic species in the Longidoroidea; it is widely distributed in Europe and has been introduced to New Zealand and the USA probably in soil adhering to planting material. Populations of this nematode have been shown to belong to the same biological species i.e. females from these populations readily crossbred with males from a Scottish population, producing viable F1 and F2 progeny. It is not known if these nematodes can crossbreed with other amphimictic nematodes in the Longidoroidea. Therefore, only the first part of Mayr's (1970) definition of a biological species has been fulfilled and the second part "reproductive isolation from other such groups" remains untested. However, the methods developed during the present study may easily be used to answer the second part of Mayr's (1970) definition of a biological species.

The application to the present study of Cronquist's (1978) definition of species reveals the weaknesses inherent in such a general definition. Luc and Southey (1970) suggest that "smallest groups" implies rejection of the sub-species concept although in nematology these are usually and quickly elevated to specific rank: "consistently" means "all, or a very large proportion, of the individuals under consideration clearly belong to one group or another, and not somewhere in between"; "persistently" means "there must be a reasonable assurance that all or a vast majority of the

offspring of members of a given species will also belong to this species, for the foreseeable future" and "ordinary means" refers to the current usage of optical microscopy. Scanning and transmission electron microscopy have been used to examine species in the Longidoroidea (Robertson and Taylor, 1975; Lamberti and Locci, 1971; Lamberti and Martelli, 1971) but these techniques have so far not been widely used in the preparation of descriptions of species. Similarly, karyological (chromosomal) and cytological studies have been done with some longidoroid nematodes (Dalmasso, 1970a, 1975; Dalmasso and Younes, 1969; Hooper, Pike and Trudgill, 1973) but such studies have not been widely used to help establish the validity of species. The present study used methods which allowed crossbreeding to be examined between amphimictic populations of longidoroids. Using this technique a population of X. diversicaudatum from central Spain was found to have a different reproductive behaviour from other populations, possibly determined by a requirement for a higher reproductive temperature. Specimens from this population were also shown to have many significant differences in their morphometrics when compared with specimens from other populations. Therefore, it seems that this population is acquiring characteristics which may eventually lead to complete reproductive isolation from other populations and thus the population may eventually be referred to separate specific rank. As the relatively new techniques become "ordinary means" several types of speciation other than morpho-species may ensue e.g. cytological-species, karyological species and biological-species. Using Cronquist's (1978) species definition involving "ordinary means" will necessitate an explanation of "ordinary means" for each newly described species.

Cronquist's (1978) terminology "smallest groups" is not appropriate for the taxonomy of longidoroid nematodes because in the

present study groups of populations of X. diversicaudatum were erected using morphometrics, reproductive ability, sex ratios and the abilities of populations to transmit viruses. The population of X. diversicaudatum from Italy consistently transmitted a strain of strawberry latent ringspot virus from Italy whereas other populations of the nematode appeared not to do so or only sporadically transmitted this virus. Therefore, the nematodes from Italy were the "smallest group". A morphometric study of populations revealed that several groups of populations could be erected depending on the degree of similarity used, of the morphometrics. With thelytokous longidoroids the smallest groups will be the progeny from females i.e. clones, which may be distinguished using cytological methods. A morphological examination of populations of X. americanum sensu lato, a thelytokous group, resulted in the erection of 25 species in the group (Lamberti and Bleve-Zacheo, 1979). Many of the species in this group were single populations which were distinguished by small differences in their respective morphometrics. Similar morphometric differences were found to occur between populations of X. diversicaudatum but these populations successfully crossbred with a Scottish population and, therefore, could not be considered separate species. The use of the terminology "smallest group" may be considered meaningless unless accompanied by its definition, the definition being dependent on the techniques used e.g. morphometrics, crossbreeding, etc.

The terminology "consistently" with its accompanying definition is not applicable to the thelytokous morpho-species which are common in the Longidoroidea. Luc and Southey (1980) examined variability in three thelytokous species of Xiphinema; X. insigne, X. elongatum and X. savanicola. The last named species is described by ibid and in their diagnosis of the species they state that X. savanicola differs from X. insigne by having a shorter tail and spear and from

X. elongatum by having a shorter spear and longer tail. However, the morphometrics of these structures overlap between the three species and thus the three species cannot be said to have specimens which clearly belong to three separate groups and not somewhere in between. Similarly, Lamberti and Bleve-Zacheo (1979) describe X. intermedium, one of the species in the X. americanum group, as occupying an intermediate position between two other species based on the morphometrics of the three species. Luc and Southey (1980) used numerical taxonomy methods to analyse statistically their data from the three Xiphinema species and the analysis revealed that the populations of nematodes formed three groups. Therefore, use of these numerical taxonomy methods would seem to offer an approach for removing much of the existing subjectivity of taxonomic classification in thelytokous longidoroid morpho-species and replacing it with much more objective methods. Similar methods applied to amphimictic longidoroids, as done with X. diversicaudatum, would also be useful for comparative purposes with the thelytokous species but need not be used to refer the amphimictic species to specific rank.

Cronquist's (1978) definition and use of "persistently" is inapplicable to the now generally accepted biological species concept. Many instances of the crossbreeding of amphimictic species and the production of fertile hybrid progeny have been recorded (Mayr, 1970). Luc and Southey (1980) assume that Cronquist (1978) meant "reproductive isolation" but, as stated earlier, this definition presents a problem when applied to thelytokous species as each individual is reproductively isolated.

Using existing, commonly available, techniques e.g. optical microscopy, it would seem that the morpho-species will continue to be applied to the Longidoroidea. However, as other techniques develop

and become more available e.g. computers for numerical taxonomy, scanning and transmission electron microscopy, karyological and cytological analyses and crossbreeding methods, it will be possible to re-examine the present subjective morpho-species more objectively. Such studies will perhaps lead to objectively described thelytokous species, possibly retaining the terminology morpho-species, and amphimictic, biological species. Furthermore, possible relationships existing between ancestral, amphimictic longidoroid nematodes and their derived clonal, thelytokous species may be examined objectively and contribute to the understanding of the evolutionary trends in the Longidoroidea.

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